Plumage Colour Function in the Narcissus Flycatcher

(キビタキの羽色の機能)

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List of publications

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Table of Contents

Introduction

History of plumage study

Why bird has striking coloration is far from a trivial question of biology (Hill and MacGraw 2006). The plumage colour of bird has been attracting scientists from more than a hundred years ago (e.g., Darwin 1871, Andersson 1994). In most bird species, males are more colorful than females, and it is generally assumed that elaborate male characters have evolved by sexual selection, because females prefer males with brighter characters, or because these characters are employed as intra-sexual selection (Darwin 1871, Andersson 1994). In contrast, female has dull plumage and this is proposed for reducing intrasexual competition and speeding up the pair formation (Hamilton 1961), avoiding predation at nests (reviewed by Badyaev & Hill 2003).

In several decades, the knowledge about plumage function and mechanism has been rapidly increasing. Mechanism studies figured out the conditional, hormonal, and genetic effects on plumage ornaments (Dawson 2004, Hill and McGraw 2006, Grindstaff *et al.* 2012). The plumages function as aposematic coloration, camouflage, and conspecific recognition (Dumbacher and Fleischer 2001, Hill and MacGraw 2006), but even now, sexual dimorphism and inter- and intra-sexual selection is the biggest issue in behavioural ecology of birds.

The ornaments such as bright plumage colour, wing length, tail length, wattle, bill colour, iris colour are considered the ornaments on birds' body. Many ornithologist and behavioural ecologists tried to identify the function of these traits with statistical models, experiments and correlation in field. While, the reason why bird has bright ornaments is not adequately understood even now (Ligon *et al.* 1998, Doucet and Montgomerie 2003, Hill and MacGraw 2006).

Multiple traits

When a female assesses the quality of a male, the possibility that mate choice is based on several ornaments on body, instead of on one, has received increasing attention in a decade (reviewed by Candolin 2003, Hebets and Papaj 2005). Many birds have several ornaments on bodies (see Møller and Pomiankowsky 1993, Johnstone 1996). Birds have different pigmental ornaments (i.e., melanin, carotenoid, structural color, depigmented white, see Hill and McGraw 2006), and different pigment has different strength and cost for expression and maintenance. For example, Carotenoid-based colors, especially the yellow xanthophylls are recognized as having an important signaling function of avian biology. Animals can only obtain the carotenoid from the diet (Goodwin 1984). The amount deposited in ornaments reflects the individual’s ability to acquire and assimilate these pigments (Peters *et al*. 2008). Therefore, carotenoid-based color signals parental ability, foraging ability, and their health (reviewed McGraw 2006a). However melanin black is not conditional trait, but it presents hormonal condition and social status (reviewed McGraw 2006b, but see also Guindre-Parker and Love 2013).

Such multiple ornaments considered as handicap hypothesis, but theoretical models have suggested that female preference for multiple ornaments and multiple handicaps are evolutionarily unstable (Schluter and Price 1993, Johnstone 1996, Iwasa and Pomiankowski 1994). Therefore patterning the evolution of multiple traits is still in a black box. Meanwhile, empirical researchers proposed four hypotheses to explain it (Møller and Pomiankowsky 1993, see also Candolin 2003, Hebets and Papaj 2005).

1) Multiple message hypothesis: Different trait gives different information about different male quality (Møller and Pomiankowsky 1993, Cadolin 2003). The basic assumption of this hypothesis is similar to the hypothesis that the display of bird has function in a limited context (Timbergen 1959, Sebeok 1977, Andersson 1980). Multiple ornaments may be maintained simultaneously when each ornament is indicating different aspect of male quality (i.e., genetic, physical condition, feeding ability, resource holding power), or represent condition-dependent traits on different timescales (Møller and Pomiankowsky 1993, Cadolin 2003). For example, ornamental colour that are made up of different pigments often exhibits different qualities; carotenoid pigments usually reflect physical condition (Hill & Montgomerie, 1994, Linville & Breitwisch, 1997, Olson & Owens, 1998, McGraw & Hill, 2000), whereas melanin-based colour mostly reflects social status (reviewed in Senar 1999, Candolin 2003, but see Fitze & Richner, 2002). The depigmented white patch convey the information of male condition about immunoglobulin levels in blood (Guindre-Parker *et al.* 2013), and social rank (Mennil *et al.* 2003).

The ornaments constructed of same pigmentation can also have different messages. For example, the depigmented the hue of white tail of Snow Bunting *Plectrophenax nivalis* correlate to the Testosteron level, but the hue of white breast correlate to immunoglobulin levels in blood (Guindre-Parker *et al.* 2013). In addition, even the one trait, the size of trait and left-right symmetry undergo different selection. (Møller 1990, Møller *et al.* 1996, Badyaev *et al.* 2001). In the experiment by Peter *et al.* (2008) revealed that if an European Greenfinch *Carduelis chloris* was supplied much lutein during the moulting period, the hue of tail became reddish, but the colouration of head and rump did not change. These results indicate the same pigmentation sometimes have different message of male quality.

In addition to this, each bird species has specific moulting schedule and strategy (Ginn and Melville 1983, Svensson 1992, Barta *et al.* 2008, Newton 2009). Some bird species have two kinds of moulting schedule in a year; one is the pre-breeding moult in wintering area, and another is the post-breeding moult in previous breeding site. The timing of moulting vary among regions and genus, while most of birds are considered having complete post breeding moulting and partial pre-breeding moulting in old world (Barta 2008). Generally, it is considered that the partial pre-breeding moulting in wintering area has evolved for wearing sexual traits for mating because they suspend remiges and rectrix. The feathers constructed in different area may convey different time scale information (Boves *et al.* 2014).

The multiple messages would evolve in species where assessing multiple aspects of the condition for mate selection and maximizing reproductive success, or those in which female has a large variation in the attention they pay to different mate quality (Candolin 2003).

2) Redundant signal hypothesis (or back-up signal hypothesis, Johnstone 1996, Møller and Pomiankowsky 1993): multiple ornaments can converge to represent the same or similar aspects of male quality for more accurate assessment of mate quality. The redundant signal hypothesize relying on one trait is imperfect way to access the quality of individual. If an error of additional signal is not correlated with an error of the signal, additional signal can increase accuracy of signal. For the receiver, the redundant signal reduced mate choice error, or reduces the time and energy for mate assessment. In addition, the redundant signal rejects dishonesty of some signals.

Møller and Pomiankowski (1993) considered the redundant signal has evolved in limited cases, such as lekking or colonial species. Candolin (2003) also argued the redundant signal is not common because the correlation of floridness between different ornaments was found only in few cases. However some empirical studies figured out the possible redundant signals in recently (Mennill *et al*. 2003, Jawor *et al.* 2004, Guindre-Parker *et al*. 2012).

3) Unreliable signal hypothesis: The unreliable signal hypothesis (Møller and Pomiankowsky 1993) proposes that multiple ornaments do not currently reflect individual condition, but evolved by female preference through Fisher process (Fisher 1930) or sensory biases (Ryan & Rand 1993). Although such trait has no direct benefit for selection and it does not have function as itself, the female preference for the trait and heritability of the trait accelerate the evolution of such trait (as in runaway selection, Eshel *et al*. 2000, Kokko *et al*., 2003).

The unreliable signal hypothesis also states the Fisher traits become ornaments having no function now (Holland & Rice, 1998, Candolin 2003, Hebets and Papaj 2005). Because the intensity of females preference on unreliable trait decrease (Møller and Pomiankowsky 1993). The plumage colour of Red Jungle fowl *Gallus gallus* is considered as such trait (Ligon *et al*. 1998).

4) Multiple receivers: The multiple receiver hypothesis assume the different signals have evolved for signalling different receiver, such as between same sex, and different sex. It is well known that not only inter-sexual selection, but the intra-sexual selection is also important in sexual selection (Smith 1972), thus different male ornament might have evolved in different selection pressure (Andersson *et* *al*. 2002, Loyau *et al*. 2005).

Hebets and Papaj (2005) and Guindre-Parker *et al*. (2012) described the multiple receiver hypothesis is an extended hypothesis of the multiple message hypothesis. I also strongly agree with this frame of thinking because if the ornament function in male-male completion, such trait should be correlated with resource holding power or territory quality, thus the message of ornaments should be received by female as the resource which the male has.

5) Combination of multiple traits: In addition to above four hypotheses, the combination of multiple traits of male plumage may not have only each function, but a combination of multiple traits has a novel function, or receivers use different trait hierarchal or in an order (Candolin 2003, Hebets and Papaj 2005). For example, the bird species having delayed plumage maturation; immature male does not express all sexual traits; thus female should recognize the delayed plumage maturation and change the sexual traits focusing. Such interaction among multiple cues can be crucial on mating choice, but it has been little studied (Candolin 2003, Hebets and Papaj 2005).

Relationship of plumage function with environment

It is essential for testing these hypotheses to consider the effect of environmental factors, because territorial birds occupy their own territory for breeding and for attracting female. The female makes her decision based on two main properties of the male: 1) the quality of resources which the male defends and 2) the quality of the male itself (Lifjeld & Slagsvold 1988). Therefore, the female choice on plumage can change on resource abundance (Alatalo 1986, Lifjeld and Slagsvold 1988).

Researchers found the sexual selection and ornament function can be different between age classes within a population (Freeman-Gallant *et al*., 2010) and habitat structure (Alatalo *et al*. 1986, Lifjeld and Slagsvold 1988). Thus, it is important to consider the environmental factors on plumage function (Taff *et al*. 2013). In other words, the environmental factors should be considered for studying plumage function in fields. It means the reproductive ecology web, the connection of these many factors correlating reproduction should be revealed (Jones and Ratterman 2009).

Material

To test the hypothesis I focused on the Narcissus Flycatcher *Ficedula narcissina*. The Narcissus Flycatcher is a small, sexually dimorphic passerine that breeds in Northeast Asia, and winters in Southeast Asia. One subspecies (Narcissus Flycatcher, *F. n. narcissina*) breeds in Japan and Sakhalin, whilst other sub-species (Ryukyu Flycatcher, *F. n. owstoni*) breeds in the Ryukyu Islands of southern Japan. The closely related Green-backed Flycatcher *F. elisae* breeds only in northern China (del Hoyo *et al*. 2006, Töpfer 2006) and is until recently considered other sub-species of the Narcissus Flycatcher. However, recent morphological, acoustic, and molecular studies have shown it to be a distinct species (Zhang *et al*. 2006).

There are some reasons why I focused on this species. First, there are so many studies on breeding biology and behavioural ecology of *Ficedula* flycatchers in Europe, especially the Pied Flycatcher *F. hypoleuca* and the Collared Flycatcher *F. albicollis* (e.g. Lundberg and Alatalo 1992, Sætre *et al*. 1997, Veen *et al*. 2001, Both *et al*. 2006, Ellegren *et al*. 2012). The taxon is sometimes treated as the model bird genus on behavioural ecology. Comparative study will reveal the specific ecological traits. Second, the Narcissus Flycatcher has sharp sexual dimorphisms. The male has clearly different color area made of depigmented keratin white, melanin black, and carotenoid yellow (Fig. 1, 2). In addition, it has delayed plumage maturation thus I can easily treat age difference and different context in ecology (i.e., experience).

Consequence

In this desertion, our objectives are to present data on (1) the life historical traits of Narcissus Flycatcher, and (2) difference of male plumage color with age and condition. Next, I show the role in male-male interaction through territory, and female mate choice on multiple male traits and territories. Lastly I comprehensively discuss function of multiple plumage color of Narcissus Flycatcher.

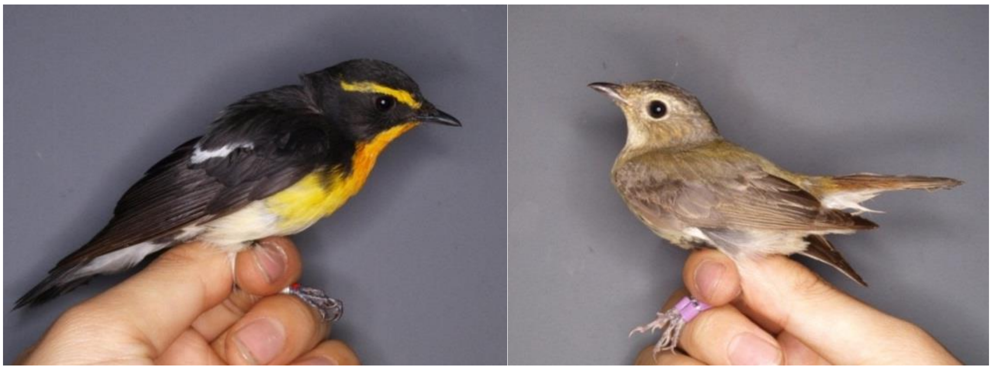


Figure 1. Male (left) and female (right) of Narcissus Flycatchers

Study site

I describe ecology of Fuji Primitive Forest for giving ecological background for study of Narcissus Flycatcher. I focused on two adjoining forests in the Fuji Primitive Forest (35°27′N, 138°38′E, 80ha, 1140m a. s. l.; average annual rainfall 1568.1 mm; annual mean temperature 10.6°C) at mountain foothill of the largest active volcano in Japan, Mount Fuji. The first was an Aokigahara basaltic lava flow, which was established in 824–826 A.D. (Chiba *et al*. 2007). The Aokigahara lava flow was created by the largest volcanic eruption of Mount Fuji in 824–826 A.D., with a total eruptive volume estimated to be more than 1.2 km^3 (Chiba *et al*. 2007). Most of the surface is similar to that of pahoehoe or rough pahoehoe lava in Hawaii (Takahashi *et al*. 2004), and the soil has only a shallow A_0 layer (Wu *et al*. 1989). On the lava flow, the evergreen coniferous forests are dominated by mature Japanese cypress (*Chamaecyparis obtuse*) and Japanese hemlock (*Tsuga sieboldii*). The second was a large forest fragment created by a lava flow (kipuka) between 1390-1120 B.C. (Ishizuka *et al*. 2007) and surrounded by the younger Aokigahara basaltic lava flow. The scoria cone in the kipuka was established in 1390–1120 B.C. (Ishida *et al*. 2007), and was not affected by the volcanic eruption in 824–826 B.C. Thu it has more abundant soil layer than the lava flow (Wu *et al*. 1989) and a smooth land surface. The deciduous broadleaved forests in the kipuka are dominated by mature Japanese oak (*Quercus crispula*), Beech (*Fagus crenata*), and Japanese beech (*F. japonica*). Both types of forest have no understory vegetation; instead, the surface is covered solely by dead leaves and mosses.

Volcanic eruption is one of the most severe natural disturbances (White 1979), and can affect species' ecology depending on its type, extent, and frequency (Fridriksson and Magnusson 1992, del Moral and Grishin 1999). Many vegetation studies have evaluated volcanic succession; however, little is known about the effects of volcanic eruptions on bird populations (Dalsgaard *et al*. 2007). Evidence of direct volcanic impacts on forest birds is available with regard to the eruptions of Mount St Helens (Butcher 1981, Hayward *et al*. 1982, Andersen and MacMahon 1986, Manuwal *et al*. 1987), Miyakejima Island (Kato and Higuchi 2003), and Montserrat (Dalsgaard *et al*. 2007). These studies have demonstrated a decline in the bird population immediately after the volcanic impact (i.e., death by ash fall, hot volcanic gas, lateral blast, pyroclastic flow, and lava). In addition to these direct effects, volcanic eruptions can indirectly affect birds; however, indirect effects have not been elucidated. For example, by scorching trees (Manuwal *et al*. 1987) and strongly disturbing land surfaces, volcanic eruptions can limit bird's nesting probability. The food abundance for birds may also be limited by differences created by the lava matrix, due to the lack of soil which insects hatch from and the instantaneous occurrence of markedly different vegetation types (Tisdale *et al*. 1965, Kamijo and Okutomi 1995, Tsuyuzaki *et al*. 1997). An evaluation of the effects of volcanic events on bird communities will facilitate an understanding of the adaption of birds in volcanic regions and important background for understanding the habitat choice and territory quality of the Narcissus Flycatcher. Here, I describe the breeding locations of bird species and arthropods abundance in the kipuka and on the younger lava flow to describe the effect prior eruption on previous ecosystems.

METHODS

Sampling arthropods

I used a white nylon insect net (diameter 60 cm) to capture arthropods on leaves and branches at a height of 3–4 m, once in a week, from the 3rd of May to the 3rd of July 2009. The branches were enclosed within the net and shaken for 30minutes to remove arthropods. Trials were conducted on sunny and cloudy days but never in the rain. Using this method I was able to capture flightless arthropods. In addition, I used six malaise traps (Hoga Products; 1.8x1.6x1.1 m) made from white nylon and using a 500-ml polyethylene bottle containing 200 ml of 30% propylene glycol to capture flying insects. I hanged the traps at 2m to avoid capturing ground dwelling arthropods. Three of the traps were placed in the kipuka and three on the lava substrate. I collected arthropods approximately once a week, from April 25th to July 4th, 2009. All traps were placed 30 m apart, with the entrances facing NNW, i.e., the same direction as the afternoon wind flow. All trapped arthropods were saturated with 70% alcohol and sorted to the level of order in the laboratory.

Breeding bird

The field study was carried out more than six hours per day starting at sunrise, more than five times per week from April 24th to August 1st 2009 and 2010. To list up the breeding bird species on two areas, I recorded the breeding activity of birds (entering cavities, carrying nest materials, or seen carrying invertebrates, and the fledglings which were fed by parents. Birds showing breeding activity were identified as the breeding birds on the area. All bird species were classified according to their food habits (insects, spiders, earthworms, seeds, plants, carnivorous) and nesting locations (ground, rock, wood cavity, and tree branch), following Nakamura and Nakamura (1995), Higuchi *et al*. (1997), and the JAVIAN database (Takagawa *et al*. 2011).

Statistical analysis

Statistical procedures followed the formulae given in R.2.12.2. (R Development Core Team 2009). To examine the difference in arthropod abundance as captured by insect nets, I used a generalized additive model (GAM, Poisson dispersion, log link). I used the “gam” of the “mgcv” package in R, with study date (smoothed Julian date from May 3rd) and study area (kipuka or lava flow) as the explanatory variables. The study date was smoothed to control for arthropod's seasonality. Significant *P* values for each factor were obtained from the likelihood ratio chi-square test of full models. Malaise traps are usable in all types of weather (Gressitt and Gressitt 1962); however, the abundance of flying insects is dependent on the weather and climatic conditions (Cooksey and Barton 1981, Briers *et al.* 2003). Therefore, I included the mean rainfall and mean hours of sunlight, using data for the duration of each trap setting, obtained from the Japan Meteorological Agency database (http://www.jma.go.jp/jma/menu/report.html). In order to examine the difference in arthropod abundance as captured by malaise traps, I used generalized additive models (GAM, Poisson dispersion, log link), with study date (smoothed Julian date from May 3rd), study area (kipuka or lava flow), mean rainfall, and mean hours of sunlight as explanatory variables. The days from before one sampling to the next was used as offset to standardize the difference in duration of trap setting, and obtained significant *P* values from the likelihood ratio chi-square test of the full model.

Differences in arthropod abundance between the kipuka and lava flow

When an insect net was used to capture arthropods, Lepidoptera were significantly more abundant in the kipuka than on the lava flow (Table 1). In contrast, Araneae were significantly more abundant on the lava flow than in the kipuka (Table 1). Other arthropods were abundant in the kipuka, but the numbers did not differ significantly from those on the lava flow (Table 1). Meanwhile, with the malaise trap method, Lepidoptera, Hymenoptera, Diptera, and Coleoptera were more abundant in the kipuka (Table 2), and the numbers of captured Diptera and Coleoptera were lower when the mean rainfall increased (Table 2).

Breeding avifauna in the kipuka and in the lava flow

A total of 20 bird species were observed to breed in the study area: 16 species nested in the kipuka whereas

14 species bred on the lava flow (Table 3). Four bird species were observed only on the lava flow, and all of them were previously described as spider-eating birds, whereas birds which eat berries tended to breed in the kipuka. In addition, ground nesters were observed to breed only in the kipuka. The wood-cavity nesters and the tree-branch nesters nested in both study areas (in the kipuka and the lava flow).

DISCUSSION

The results of our study suggest that prior volcanic eruption may have two types of effects on previous breeding avifauna through changes in (1) food availability and (2) nest-site availability. With regard to food availability, I recorded abundant insects and insectivorous birds in the kipuka but not on the lava flow. It is widely described that insect abundance is influenced by vegetation. In volcanic regions, the vegetation is dependent on the soil matrix, and the abundance of arthropods is likely limited by the vegetation (Kamijo and Okutomi 1995, Tsuyuzaki *et al*. 1997, Parmenter *et al*. 2005). The kipuka has broadleaf forest while the younger lava flow has stands of coniferous forest. Thus, arthropods abundance may also be influenced by vegetation. In addition, many arthropods require soil to reproduce, and thus the low abundance of arthropods on the lava flow might be a result of the lack of soil on that substrate (Parmenter *et al*. 2005). One group of arthropods, spiders, was more abundant on the lava flow than in the kipuka. I found that the evergreen coniferous forests on the lava flow had abundant spiders, similar to other studies (Forstmeier and Keßler 2001, Mizutani 2002). Spider eating birds were likely to breed there. These results might mean that only spider eating birds can breed in low arthropods abundant area on the lava flow.

I also found that ground nesting species nested only in the kipuka whereas rock nesters nested only on the lava flow. Ground nesters usually build their nests in the soil or on the soil surface; therefore, the lack of soil on the lava flow might limit their breeding area. It has also been found that predation of ground nests increases in volcanically disturbed areas (Andersen and MacMahon 1986); thus there might be other reasons for the lack of ground nesters in this study. Wood-cavity and tree-branch nesters were not affected by the condition of the soil surface, because abundant wood cavities and trees were present in both areas (Y. Okahisa unpubl. data). In sum, these results suggest that the eruption creates different breeding avifauna according to the nest site characteristics.

In the present study, I have described that volcanic disturbances affect insect abundance and breeding avifauna, even hundreds of years after the eruption. As is generally described, the breeding avifauna changes depending on habitat structure (Sherry and Holmes 1985), thus alternation of avian habitat would be expected to lead to dramatic and unpredictable changes in bird species composition and abundance patterns across disturbance-modified landscape (Swanson *et al*. 2005).

For the Narcissus Flycatcher, the prey abundance is much higher in the kipuka, while they bred both areas. This is probably because the abundant nest sites (dead trees) in both areas. The secondary whole nesters were also observed in both areas; thus the abundance of competitor for nest site may not be so widely different between two areas.

Table 1. Differences in insect abundance between study areas (kipuka and lava flow) for insects captured by nets

Order	Lava flow estimate (*P*)[a]	Smoothed Julian date (*P*)
Dermaptera	-129.7 (1.000)	0.862
Hemiptera	-0.014 (0.867)	**<0.001**
Lepidoptera	**-1.145 (0.008)**	0.065
Hymenoptera	-1.946 (0.068)	0.890
Formicidae	-0.337 (0.416)	**0.014**
Phasmatodea	-135.9 (1.000)	0.251
Araneae	**0.3024 (<0.001)**	**<0.001**
Opiliones	-0.025 (0.912)	**<0.001**
Orthoptera	0.363 (0.265)	0.055
Ephemeroptera	-0.047 (0.829)	**<0.001**
Coleoptera	-0.002 (0.974)	**<0.001**

[a] Lava flow estimates indicate relative numbers compared to the kipuka in the generalized additive model (GAM; Poisson dispersion; only the Julian date is smoothed). Significant *P* values were obtained from the likelihood ratio test of full models. All bold type means the variables significantly affect the arthropod abundances.

Table 2. Differences in insect abundance between study areas (Kipuka and lava flow), for insects captured by malaise traps.

Order	Lava flow estimate (*P*)[a]	Mean rainfall estimate (*P*)	Hours of sunlight estimate (*P*)	Smoothed Julian date (*P*)
Diptera	**-0.685 (<0.001)**	**-0.019 (0.038)**	0.012 (0.768)	**<0.001**
Hemiptera	0.049 (0.384)	0.019 (0.623)	0.130 (0.443)	**<0.001**
Lepidoptera	**-0.748 (<0.001)**	-0.018 (0.478)	-0.213 (0.082)	**<0.001**
Hymenoptera	**-1.112 (<0.001)**	-0.020 (0.472)	-0.014 (0.910)	**<0.001**
Coleoptera	**-0.614 (<0.001)**	**-0.021 (0.002)**	-0.013 (0.689)	**<0.001**

[a] Lava flow estimates indicate relative numbers compared to the kipuka in the generalized additive model (GAM; Poisson dispersion; only the Julian date is smoothed). Significant P-values were obtained from the likelihood ratio test of full models. All bold types mean the variables significantly affect the insect abundances.

Table 3. Breeding bird species in Fuji primitive forest. I describe only the presence / absence of bird species on a lava flow and in kipuka.

Species	On lava flow	In kipuka	Food habit[a]			Nesting location[b]
			Insects	Spiders	Others	
Regulus regulus	●		●	●		T
Certhia familiaris	●		●	●		C
Troglodytes troglodytes	●		●	●		R
Aegithalos caudatus	●		●	●	Berries	T
Sphenurus sieboldii		●			Berries	T
Luscinia cyane		●	●	●		G
Turdus cardis		●	●		Earthworms	T
Anthus hodgsoni		●	●			G
Phylloscopus coronatus		●	●			G
Parus major		●	●	●	Berries, seeds	C
Picus awokera	●	●	●			C
Dendrocopos major	●	●	●	●	Berries	C
Turdus chrysolaus	●	●	●	●	Earthworms	T
Ficedula narcissina	●	●	●	●		C
Cyanoptila cyanomelana	●	●	●			T, R
Muscicapa dauurica	●	●	●			T
Parus varius	●	●	●	●	Berries, seeds	C
Parus montanus	●	●	●		Seeds	C
Parus ater	●	●	●		Seeds	C
Sitta europaea	●	●	●	●	Seeds	C

[a] Food habit and nesting location were classified following Nakamura and Nakamura (1995), and Higuchi *et al*. (1997).

[b] T, tree branch; C, wood cavity; R, rock; G, ground.

Chapter I

Breeding ecology of Narcissus Flycatcher

Phylogenetic analysis has revealed that the *Ficedula* genus evolved in the Oriental region (Outlaw and Voelker 2008); however, there is insufficient information on the ecology of *Ficedula* flycatchers in the Oriental region. In most *Ficedula* flycatchers, even basic breeding ecology has never been described. On the other hand, there are a huge number of studies on the breeding biology and behavioural ecology of *Ficedula* in Europe, particularly the Pied Flycatcher *F. hypoleuca* and the Collared Flycatcher *F. albicollis* (e.g. Lundberg and Alatalo 1992, Sætre *et al*. 1997, Veen *et al.* 2001, Both *et al.* 2006, Ellegren *et al.* 2012). Studies on a clade of the Pied Flycatcher, Collared Flycatcher, Atlas Flycatcher *F. speculigera*, and Semi-collared Flycatcher *F. semitorquata* have informed the ecology of flycatchers and their evolutionary biology; however, these are only four species of the 30 *Ficedula* flycatchers separated from the Oriental region (Sætre *et al*. 2001, del Hoyo *et al.* 2006).

Ecological traits, behaviours, and morphology generally evolve depending on environmental conditions (Böhning-Gaese and Oberrath 1999, Sætre & Sæther 2010); characteristics of *Ficedula* flycatchers were also influenced by evolutionary history (e.g. Outlaw 2011). Therefore, comparing life history traits is important for figuring out the evolution of the *Ficedula* genus. In other words, we need to determine life history traits and describe the breeding ecology of *Ficedula* flycatchers.

The Narcissus Flycatcher is a migrating flycatcher breeds in East Asia. Breeding ecology and natural nest sites of the flycatcher have never been described. Narcissus Flycatchers prefer to nest in dense deciduous and mixed forest (Fujimaki 2007). It is considered as socially monogamous (Nakamura and Nakamura 1995). It mainly forages on arthropods, including caterpillars, spiders, and other small invertebrates (Murakami 1998) and use deep nest-boxes with small entrances (Hyuga 1952; Suzuki *et al*. 1992) when these are supplied. However the knowledge from nest-box population on their ecology and natural history does not accurately reflect the facts in nature (e.g., Karlsson & Nilsson 1977, Slagsvold 1987). For example, nest-box populations may have higher population densities than natural populations because nest boxes can be placed at higher densities than cavities may occur in natural habitats. Therefore, nest-box populations may not properly represent natural bird populations (e.g. McComb & Noble 1981, Purcell *et al*. 1997). Moreover, evolutionary interpretations of the results gained from nest-box studies should be tempered with observations of birds in their natural habitats. Such realizations have recently led to the description of natural nest sites of flycatchers (Czeszczewik & Walankiewicz 2003, Walankiewicz *et al*. 2007, Wang *et al*. 2007b, Wang *et al*. 2008).

The closely related Green-backed Flycatcher *F. elisae* breeds only in northern China (del Hoyo *et al*. 2006, Töpfer 2006), and the breeding ecology of this bird was described as the breeding ecology of the Narcissus Flycatcher (Wang *et al*. 2008) because the Green-backed Flycatcher was until recently considered other sub-species of the Narcissus Flycatcher. However, recent morphological, acoustic, and molecular studies have shown it to be a distinct species (Zhang *et al*. 2006). In fact, the breeding ecology of the Narcissus Flycatcher has never described in detail.

Our objectives of this study are to present data on (1) the reproductive seasonality and life historical traits, (2) the nesting habits, and (3) the reproductive behaviour of the Narcissus Flycatcher. Lastly, I discuss the breeding ecology of the Narcissus Flycatcher in comparison to the other

Ficedula species.

STUDY AREA AND METHODS

Field study was carried out between the end of April and the end of August 2009–2013 in the Fuji Primitive Forest (35°27′N, 138°38′E, 1,140 m above sea level, Yamanashi Prefecture, Japan).

For assessing the breeding density in the forest, route censuses were conducted using conspecific song playback to locate territorial birds after all flycatchers settled their territories in end of May to July in 2012. I used a song which I had previously recorded in our study area and censused all parts of our study area, stopping every 50 m to playback song and record the location of birds using a handheld GPS unit (accuracy ± 8 m, eTrex Legend HCx, Garmin Ltd., Olathe, Kansas, USA).

Other field work was conducted in the main study site. For estimating territory size, territory mapping was conducted. I searched for singing males in the study area every morning (03:30–11:30 h) during the study periods. When a singing male was found, I followed it and plotted the singing location on maps. I located singing points by colour markings on the trees (every 20 m) that were made prior to the spring migration of Narcissus Flycatchers, and each marking was located with GPS. Each observation trial was only 5 min in duration, which was repeated daily. Eighteen trials were needed to assess 90% of the territory. Thus, I only used individuals observed singing in more than 18 trials to estimate territory size. Finally, I calculated the minimum convex polygon of song locations using ArcGIS 10.1 (ESRI Inc., Redlands, CA, USA) and considered this to be the flycatcher’s territory.

In addition, singing males were searched in the study area every day (03:30–19:00 h) during the study period. The day that a male was first recorded singing in a territory was assumed as his arrival day (Mitrus 2007a, Okahisa *et al*. 2013). The pairing dates were determined by observation of males and females engaged in a contact call and moving together. The number of males that females visit on the arrival date was estimated by the observation of two philopatric already ringed females and a female captured in the dawn of arrival day.

I also described the behaviour of individuals among study periods, and also included information from occasional observations at other times. Each of the individuals was lured into mist nets using song playback or at water puddles. Individuals were ringed using a combination of aluminium (authorized by the Japan Environment Agency) and unique colour-coded rings (A.C. Hughes, UK) for individual identification in the field.

Nests were located by following male and female exhibiting nesting-building behavior (such as entering holes and crevices, and carrying plant fibers) or seen carrying invertebrates with which to feed their nestlings. Areas where adults were heard giving alarm calls were also intensively searched, facilitating the finding of nest holes in both high and low locations (Wang *et al*. 2008). Upon finding a nest the following data were collected: (1) tree species, (2) nest site type (half cavity, full cavity, chimney, or shelf; Fig. 3), (3) height of nest entrance above ground (as measured by laser rangefinder; Laser 550A S, Nikon), (4) orientation of the entrance (to the nearest 45°), (5) condition of nest tree fragment with the cavity (live or dead), (6) diameter of tree trunk at breast height (DBH, as measured by tape), (7) the narrowest and widest entrance diameter (measured by ruler), (8) the narrowest and widest nest hole inner diameter (measured by ruler and tape measure), (9) hole depth (the vertical distance between the lower edge of the entrance and the middle of the hole bottom; measured by ruler), (10) the inner diameter and nest cup depth (measured by ruler), and (11) forest type at nest site (deciduous broadleaf forest or coniferous evergreen forest). When nest holes were very high or located in fragile fragments of dead trees, it was not possible to measure the entrance diameter and cavity size. The vegetation characteristics of Narcissus Flycatcher habitat were described in 20 randomly placed 10 m quadrats in each forest type (deciduous broadleaf and coniferous evergreen). The number of each tree species and their DBH values were recorded for each quadrat. Nests were monitored every 2–3 days with a digital camera on a long pole. In cases where the nest was predated upon before the female began incubation or where the nest was found during the nestling stage, I was unable to determine clutch size. Conversely, when the nest was predated upon before egg hatching, I could only record clutch size.

To reduce the human pressure on reproduction of the flycatcher, I captured the nestling at only two nests. In addition, I did not conduct any experiments at the site. The site is a native primitive forest (Okahisa *et al*. 2014 for detail), thus the anthropogenic effect was limited.

Statistical procedures follow the formulae given in R.2.14.0. (R development core team 2011). To examine the effects of tree species and forest types on nest height and DBH, I used generalized linear models (GLM) with gaussian errors with identity link function. I also used multinomial logistic regression models with ‘multinom’ function in the ‘nnet’ package when I tested the effect of tree species, tree height and DBH on flycatcher’s nest types. Significant p-values for each factor were obtained from likelihood ratio tests comparing the likelihood of the model including the factor and that of the model, not including the factor. Binomial distribution Generalized Additive Mixed Model (GAMM) with ‘gamm4’ function in the ‘gamm4’ package, were performed when I tested the effect of DBH, condition of the tree (live or dead), and tree species on the nest site preferences of flycatchers. In this method, forest types are included as random effects and all models are ranked from best to worst based on Akaike's Information Criteria (AIC). Chi-square tests were performed to determine if flycatchers prefer a particular nest entrance orientation, in this case the null hypothesis was that flycatchers use all orientations equally.

RESULTS

Population in the Fuji Primitive Forest

In the course of the wide area census, 373 males were observed defending territories in 13.92 km2 of the forest. The breeding density was 0.26 individuals/ha in the forest. The breeding density in the main study area was 0.55 ± 0.11 individuals/ha (mean of study years ± SD; range 0.43–0.71 individuals/ha). The territory size of the male flycatcher was 1.13 ± 0. 66 ha (mean ± SD; n = 128) at the main site. In total 33.91 ± 18.74 % of males returned to the site in the next year (n = 115), whereas the return rate differed between years (range 14.63–58.97%). Polyterritoriality was never observed.

Arrival and pair formation

I monitored breeding activity of 105 pairs and found 65 nests in the 5 years of the study. The breeding period of the Narcissus Flycatcher starts from the arrival of the males. The males arrived at the breeding sites earlier than the females (Fig. 1, T-test; t = -10.23; df = 138.78; P < 0.001). The males arrived on 30 April ± 4.87 days (mean ± SD; n = 105), and the females arrived on 10 May ± 19.02 days (mean ± SD; n = 76). On the arrival day, the females visited the territories of at least three males (n = 3) and decided on a partner. They paired on 10 May ± 19.02 days (mean ± SD; n = 76).

The display behaviour of male Narcissus Flycatchers was observed when males were attempting to attract females. Males displayed their breast plumage to the females, raising their heads and shaking them slowly and smoothly from side to side. In addition, males flew around the females in a ‘∞’-shaped display flight (Okahisa 2014), making a ‘din-din-din’ call (Kajimoto 2009a). After the display, the male flew back to his territory with a wavy, fluttering flight. When a female accepted a male, the female smoothly wagged her tail. Conversely, when she rejected a male, the female made jumps to escape the male display. On only one occasion did I observe a female dancing with the display behaviour typical of the male. After pair formation, pairs moved around the territory, conducting contact calls.

From the arrival date of each male through the copulation period, male-male interactions were observed. Typically, the dominant male stood just in front of the intruder, and they gazed at each other. Sometimes they cracked bills and made clicking sounds. The dominant male made vocalizations to threaten the intruder (Kajimoto 2009b). Next, the males chased each other and directly pecked each other’s breasts. The fight occurred high in the trees or the males gradually climbed up the tree by jumping onto higher branches during the fight. When the fight escalated, males pecked each other while hovering in the air, and both males fell to the ground.

In the five study years, four female-female interactions were observed. In three cases, an intruder visited a territory where the paring had already occurred, and one occurred the day the two females were firstly observed. In all cases, the dominant female found the intruder; the dominant female made a dash at the intruder. The male also made a dash at the dominant female and intruder females. The intruder always made an escape flight from the attack of the dominant partners. I never observed the intruder attacked the dominant female or stayed in the same territory after being attacked, and polygamy was never observed.

Nest building

After pair formation, the pairs started searching for a nest site. The pairs flew around the territory and checked wood cavities while making contact calls. In most cases, the male flew after the female, but males also escorted females to nest sites by perching in the entrance of a wood cavity and turning to face the female similar to the Pied Flycatcher (Lundberg and Alatalo 1992). Females inspected the inside of the cavity. In three cases, the male attacked the female before or after she went inside. Once the female decided on the nest site, she began building the nest by alone. After the pair formation, the female started nest building on 12 May ± 19.91 days (mean ± SD, n = 36). Most nests were constructed in the half cavity (Okahisa *et al*. 2012). The nest depth was so shallow that the eyes and the bill of the female were normally visible from the entrance. They were commonly made from dead leaves, moss, plant fibre, and animal hair (Okahisa *et al.* 2012). Normally, nest building took 4.0 ± 1.07 days (mean ± SD, range = 2–10; n = 15). One nest was abandoned; the male of the pair attacked the female when she finished bringing nest material and then appeared outside the nest.

Nest sites and nest characteristics

A total of 41 nests was found and measured in three breeding seasons (only three were used twice); 24 in broadleaf forest and 17 in coniferous forest. Most nests (61.0%, N=25) were located in half cavities whereas 22.0% (N=9) were in full cavities, 9.7% (N=4) were built in chimneys, and 7.3% (N=3) were on shelves. Japanese Hemlock was the most commonly used tree species for nests

(N=11). Other tree species used for nests were Siebold's Beech (N=5), Japanese Cypress (N=5), and Hill Cherry *Cerasus jamasakura* (N=4), with eleven other species used only once or twice (Fig. 4). Narcissus Flycatchers did not show significant nest tree species preferences (Table 1). The DBH ranged from 39 to 381 cm (mean±SD: 97.1±61.5, N=41, Fig. 5) and they significantly disliked nesting in trees with DBHs of less than 20 cm (Fig. 6; Tables 1 & 2). Differences in the diameters of nesting trees did not differ significantly between tree species (GLM; tree species, deviance=65,570, df=14, P=0.303). Dead trees and living trees were used at similar rates (Dead 51%, Living 49%, N=41), while Narcissus Flycatchers prefer to nest in dead trees (Fig. 7, Tables 1 & 2). The average nest height was 7.3 m and more than 90% of nests were between 2 and 12 m (Fig. 8). The highest nests were in Siebold's Beech trees, but nest heights did not differ significantly among 15 tree species or between forest types (GLM; tree species, deviance=186.85, df=14, P=0.786, forest types, deviance=10.13, df=1, P=0.469). Nest type was related to neither tree species (Multinomial regression model, tree species vs Null, deviance=35.033, df=42, P=0.768) nor height above the ground (Multinomial regression model, tree species vs Null, deviance=3.099, df=3, P=0.376). However, there was a significant tendency for shelf nests, rather than the other three nest types, to be present on larger trees (Multinomial regression model, DBH vs Null, deviance=9.059, df=3, P=0.02).

The most common nesting materials used were dead leaves, mosses, plant fibers, and animal hairs. The average nest cup diameter was 6.50±0.37 cm (N=16), and the average net cup depth was 3.24±0.71 cm (N=16). Nests were built in shallow cavities (mean depth±SD: 7.00±4.24 cm, N=16) with a small bottom area (mean hole greatest diameter±SD: 9.85±1.37 cm, mean hole smallest diameter±SD: 8.26±1.34 cm, N=17). The maximum entrance diameter ranged between 4.5 and 200 cm (mean±SD: 26.44±45.56 cm, N=17) and the minimum entrance diameter ranged between 3.0 and 12.0 cm (mean±SD: 7.41±2.20 cm, N=17). Most of the entrance holes were orientated either North or South (Fig. 9) and differed significantly from expectations of chance ($\chi 2=18.00$, df=7, $P<0.05$).

Productivity

The first egg was laid on 19 May ± 15.23 days (mean ± SD; n = 12), hatched on 6 June ± 23.93 days (mean ± SD; n = 17), and chicks fledged on 20 June ± 36.92 days (mean ± SD; n = 33). All females initiated incubation after the clutches were complete; all incubation was undertaken by the female and the chicks were hatched synchronously. One egg was laid each day. The colour of the eggs was bluish-white with reddish brown spots on the shell, similar to that previously described (Suzuki 2011). In most nests, males approached the nest less than once a day and upon approach merely observed the situation of the nest. Sometimes the males did not enter the nest, but rather hovered in front of the nest and looked at the female. Females were often absent from the nest probably on account of foraging. The female sometimes exposed her face from the entrance when she nested in the deep cavity with a small entrance. The mean incubation period was 12.0 ± 4.09 days (mean ± SD; range = 10–13; n = 7). The clutch size was 4.63 ± 0.70 (mean ± SD, Fig. 2; n = 41), and 96.8% of the eggs hatched (n = 125).

The chicks were naked and blind at hatching. They had pinkish-yellow skins. The nestlings rapidly increased in body weight until the weight increase levelled off. They reached the same weight as adults (13 g) in 7.0 ± 1.00 days (mean ± SD; range 6–8; n = 8). When the nestlings were 2 days old, the feather sheaths looked like dots in the skin. The primary and secondary sheaths broke in 6 days and the feathers grew rapidly. The wing feathers were fully grown within 10–11 days, but tail feathers were still growing even after fledging. The nestlings needed an average 11.0 ± 3.42 days (mean ± SD; range = 10–12; n = 23) to fledge. The mean brood size was 4.35 ± 0.69 (mean ± SD; n = 34), and the mean number of fledglings was 4.29 ± 0.69 (n = 24). I never observed death by starvation, although 26% of the nests were predated and 2% of nests were lost to tree fall (n = 65).

Both parents of the Narcissus Flycatcher made a long-lasting ‘pik-pik-pik’ alarm call (Hirano 2009) in the incubation stage, breeding stage, and when feeding fledglings. The intensity of the alarm call became stronger when the chicks grew up or when predators approached such as a Eurasian jay, Garrulus glandarius, and an Ural Owl, Strix uralensis.

When a predator or human approached the females in their nests, the females fell from their nests to the ground to escape predation. Initially, they did not flutter their wings but just kicked the nest and fell down towards the ground. Near the ground, they spread their wings and changed posture. Thereafter, they flew along the surface of the ground. The behaviour was observed in most of the nests during nest checking or when the tree was accidentally shaken by the observer.

The fledglings were observed for 7.83 ± 2.13 days (mean ± SD; n = 23) after fledging, though this number was obviously influenced by observation bias and predation. At maximum, fledglings stayed in the territory for 19 days (range = 2–19) and were fed by their parents.

Double brood

Although there were a few double broods, I could not find any nest by double brood. The fledglings by re-nesting or second broods were observed in mid-summer (July 24 to August 15; n = 23). Using only six cases, I determined that fledglings were second broods because I observed the first fledgling of the pair. The fledglings of the second broods were observed 44.5 ± 6.10 days (mean ± SD; range = 32–50; n = 6) after the first fledging of the pair. During the double brood, only the female fed the fledglings, and feeding of fledglings by males was never observed.

On five occasions, predation of fledglings by Ural Owls was observed. In addition, Narcissus Flycatchers routinely strongly mobbed these owls. Additionally, the parents, some other males, and a Siberian Robin, Luscinia cyane, approached and sometimes pecked the fledglings.

DISCUSSION

Life history trait and behaviour

The clutch size of the Narcissus Flycatcher is smaller than the clutch sizes of other *Ficedula* Flycatchers (Table 3). It is well known that the birds have smaller clutch size at lower latitudes (Cardillo 2002, Jetz *et al*. 2008). The Narcissus Flycatcher breeds in lower latitudes than other migrating flycatchers and, similarly, other *Ficedula* flycatchers breeding in lower latitude have smaller clutch sizes (e.g. Green-backed and Atlas Flycatcher) than those breeding at higher latitudes (Table 3). Therefore, the latitudinal difference is likely to affect this life history trait of the Narcissus Flycatcher.

In addition to the latitudinal effect, the prey abundance (Lack 1947), size of nest site (Karlsson and Nilsson 1977), and predation (Slagsvold 1982) influence clutch size (reviewed by

Godfray *et al.* 1991). First, the food resource limitation was considerable, whereas I could not observe death of chick by starvation in the Narcissus Flycatcher, similar to the other flycatchers with small clutch sizes (Table 3). Thus, the food resource limitation might not have influenced the clutch size of the Narcissus Flycatcher at the site. Second, Narcissus Flycatchers mainly nests in a shallow cavity with a wide entrance, similar to the Red-breasted Flycatcher (Okahisa *et al.* 2012, Mitrus and Soćko 2004), and is not concealed; thus, the nest size is not strictly limited. The nest size limitation would not be an appropriate hypothesis to explain the trend in clutch size. Lastly, it is known that a higher predation rate decreases the clutch size of birds (Slagsvold 1982), because a small clutch size saves energy for renesting attempts to follow failure and to reduce the predator's chance to detect nest location (Slagsvold 1982). The predation rate in the site was 26%; it is not higher than other flycatchers in natural cavities in old growth forest (e.g., Red-breasted Flycatcher 40%, Mitrus and Soćko 2004; Pied Flycatcher 49%, Czeszczewik and Walankiewicz 2003). Therefore, the clutch size in the study site would not be strongly influenced by the prey abundance, size of nest site, and predation. The results of this study are likely to reflect the species' characteristics.

The Narcissus Flycatcher has comparatively smaller clutch size than other flycatchers, but the number of fledglings was not fewer than those of other species. The average number of fledglings in this study (4.29 ± 0.69) was similar to that of the Atlas Flycatcher (4.37 ± 1.40, Boudeffa 2014), Yellow-rumped Flycatcher (4.13, Deng *et al.* 2010), Pied Flycatcher (range 2.94–5.56, Lundberg and Alatalo 1992), and Collared Flycatcher (4.2–5.5; Mitrus 2003). This is because there was a high hatching success and no brood reduction.

Compared with other *Ficedula* flycatchers, the Narcissus Flycatcher has shorter nest building, incubation, and nestling periods. This trend could be caused by their small clutch size and adaptation to nest predation. Small clutch size shortens the incubation and nestling periods (Martin 1995). It reduces feeding costs and allows nestlings to grow rapidly (Royama 1966, Ricklefs 1968, Slagsvold 1982). Narcissus Flycatcher nestlings rapidly gained weight, and in some cases, nestlings weighed 13.0 g just 7 days after hatching. These results suggest that the Narcissus Flycatcher reduces the cost of each breeding by limiting clutch size, thereby minimizing nestling losses, increasing the likelihood of breeding whole clutches, and successfully shortens the breeding period. In this regard, however, the other flycatchers with a smaller clutch size do not have such a short breeding period as the Narcissus Flycatcher. This indicates not only the small clutch size but also other factors that affect the short breeding season of the Narcissus Flycatcher.

The Narcissus Flycatcher nests in shallow cavities with a wide entrance (Okahisa *et al*. 2012). Consequently, such nests are much more exposed than those of other cavity-nesting species (Mitrus and Soćko 2008), and they are likely to suffer more nest predation than typical cavity nesters. Ornithologists have previously reported that concealed nest sites are much safer than exposed nest sites (Ricklefs 1969). Thus, the natural pressure from nest predation might be stronger than that for other cavity nesters. Shortening the nestling period might be an efficient way to circumvent this increased nest predation because less energy is expended for breeding, thus the energy reserves are available for the double brood (Slagsvold 1982). In addition, shortening the incubation and nestling period has an advantage of reducing the possibility that the nest is found by predators (Slagsvold 1982). The Red-breasted Flycatcher nests in similar shallow cavities (Mitrus and Soćko 2004), although sometimes, the short nestling period (11 days, Table 3) also suggests that the exposed nest site is correlated with the shortening of the nestling period.

Such nest structure might cause higher nest predation pressure, but it allows incubating females a clear view of their surroundings (Mitrus and Soćko 2008) because the nest depth is so shallow, and thus the eyes and bill of the female is normally visible from the entrance. For observation, a female sometimes exposes her face from the entrance when she nests in a deep cavity with a small entrance, which also suggests that females prefer such nest sites to more effectively detect nest predators. Actually, the female responds sensitively to the approach of predators and humans. Females have a unique escape behaviours, such as falling from their nests to the ground to escape predation. The nest site therefore allows the female to escape from predators.

In contrast to the shorter incubation and nestling period, Narcissus Flycatcher fledglings were fed by their parents for an extended period of time (19 days maximum). This may be longer than other *Ficedula* flycatchers (Table 3). The long parental care is typically found in the tropical region, and it is considered as an adaptation of a life history trait to the long life span, high nest predation (Stutchbury and Morton 2001). The longer parental care of Narcissus Flycatcher might be correlated with the breeding in comparatively lower latitudes than other flycatchers. However, tropical birds generally have longer incubation and nestling periods. This is in contrast to the short incubation and nestling periods of the Narcissus Flycatcher. Therefore, the longer care for the fledgling may indicate that while the Narcissus Flycatcher has succeeded in shortening the nestling period, it had to extend the period of feeding for fledglings. Fledglings were preyed upon by Ural Owls, although the short incubation, short nestling period, and long care for the fledglings suggest that nest predation is more detrimental than fledgling predation.

In the behaviours, the alarming call and male-male interactions were notable. Similar to other *Ficedula* Flycatchers (e.g., the Pied Flycatcher; Krama and Krams 2004), the Narcissus Flycatcher has a long-lasting alarm call. Krams *et al*. (2007) suggested that such a mobbing call could cause a predator to leave the vicinity, but may also attract predators to the nest. Krams *et al*. (2008, 2009) reported the mobbing behaviour of the Pied Flycatcher is a conspecific reciprocal altruism mechanism of the semi-colonial social system. The observation of a long-lasting alarm call performed by the Narcissus Flycatcher suggests that they may construct a semi-colonial social system similar to that of the Pied Flycatcher (Krams *et al*. 2009). It is unclear why the Narcissus Flycatcher always makes a call, but the observation that a male drew a predator away from the nest suggests there is some benefit in calling to avoid nest predation. Further behavioural studies are required.

Male-male interactions and male display seem to be correlated with the bright orange plumage colour on the breast of the male. The bright plumage on the throat is a common trait of the *Ficedula* Flycatchers, e.g. Red-breasted Flycatcher, Mugimaki Flycatcher *F. mugimaki*, and Rufous-chested Flycatcher *F.dumetoria* (del Hoyo *et al*. 2006). It has been previously suggested the breast red patch is a status signal of Red-breasted Flycatcher (Mitrus 2007b). These findings suggest that the patch may have some effect on mate selection and male dominance of Narcissus Flycatcher. Behavioural studies focusing on the alarm call and bright patch are thus required.

Nest site and nest

Narcissus Flycatchers nest in small deep cavities and on shelves (this study), whereas the closely related Green-backed Flycatcher mainly nests in shallow open cavities, chimneys, and in branch junctions (Wang *et al*. 2007b, Wang *et al*. 2008), thus despite being closely related these two flycatcher species select different nest sites. Some natural nest types of Narcissus Flycatcher are very similar to those of other *Ficedula* flycatchers, such as the Collared Flycatcher and Pied Flycatchers , both of which prefer deep cavities with small entrances (Czeszczewik & Walankiewicz 2003; Walankiewicz *et al*. 2007), and especially the Red-breasted Flycatcher, which prefers half cavities with a wide entrance, chimneys, and shelves (Mitrus & Sock 2004).

Normally, *Ficedula* flycatchers prefer to nest in live trees (Wesołowski 1989, Czeszczewik & Walankiewicz 2003), but both Narcissus and Green-backed flycatchers often nest in dead trees, despite nest failure due to dead trees falling down (Wang *et al*. 2007b, Wang *et al*. 2008), and Narcissus Flycatchers prefer to nest in thick trees. Mature trees (dead and thicker) often had some wood cavities in the study area (Ayaka Sasaki unpublished), and therefore the results may have been related to the natural abundance of cavities. In addition, the greatest diameters of Narcissus Flycatcher's nests were 9.9±1.4 cm, and they disliked nesting in trees with DBHs of less than 20 cm. This result suggests nest site availability is limited by DBH.

Narcissus Flycatchers were only rarely found to use the same nest site twice, but no differences could be found between the nest sites used once and those used twice. These results suggest that either nest sites were abundant in the study area, or that there is some benefit in changing nest sites between seasons. *Ficedula* flycatchers typically avoid nesting repeatedly in the same site (Mitrus & Sock 2004, Wang *et al*. 2007b), although the reasons remain unclear. It is possible that they select different nest sites so as to avoid nest predation (Mitrus & Sock 2004) or ectoparasite infections (reviewed by Mazgajski 2007).

Narcissus Flycatchers in Japan tended to nest higher and in more mature (i.e., thicker) trees than Green-backed Flycatchers in China (Table 4). Green-backed Flycatchers use lower nest sites than Yellow-rumped Flycatchers *F. zanthopygia* and other secondary cavity- nesting passerines such as tits (*Poecile spp.*) and nuthatches (*Sitta spp.*). Green-backed Flycatchers breed sympatrically with these other species, which means that they may face intense inter-specific competition for nest sites (Wang *et al*. 2008). In Fuji Primitive Forest, the Narcissus Flycatcher has few number of competitors for nest cavities (tits and nuthatches) allowing it to monopolize preferred nest sites. There are also differences in the predator assemblages between the Japanese and Chinese sites that could affect nest locations. The area where Green-backed Flycatchers nest have Swinhoe's Striped Squirrels *Tamiops swinhoei*, Rock Squirrels *Otospermophilus variegatus*, Siberian Weasels *Mustela sibirica*, Japanese Sparrowhawks *Accipiter gularis*, Great Spotted Woodpeckers *Dendrocopos major*, Eurasian Jays *Garrulus glandarius*, Red-billed Blue Magpies *Urocissa erythrorhyncha*, and Chifeng Beauty Snakes *Elaphe anomala*. However, there does not seem to be any relationship between predator type and nest height (Wang *et al*. 2007b). Conversely, Fuji Primitive Forest has Japanese Marten *Melampus melampus*, Japanese Rat Snake *E. climacophora*, Eurasian Sparrowhawk *A. nisus*, Japanese Sparrowhawk, and Great Spotted Woodpecker *Dendrocopos major*, Eurasian Jay, and Jungle Crow *Corvus macrorhynchos* although martens seemed to be the dominant predators at this site (Gen Morimoto & Yuji Okahisa. unpublished). Both martens and snakes climb trees to access nests, thus building higher nests may be an anti-predator strategy. The reasons for the difference in nest site characteristics between Narcissus and Green-backed flycatchers are likely to be complex, but they are likely to include differences in forest composition, and predator assemblages, and species specific differences in behaviour (Wang *et al*. 2007b).

It is known that birds can choose very specific orientations for their nests (e.g., Finch 1983, Hoekman *et al*. 2002, Burton 2006). Most Narcissus Flycatcher nest-holes of were oriented either North or South, as was also the case for the Green-backed Flycatcher (Wang *et al*. 2007b), suggesting that nest site opening orientation is highly conserved between the two species or that there is a common environmental factor affecting them both.

There was no difference in the minimum nest entrance diameter between Narcissus Flycatchers and Green-backed Flycatchers (Table 4). This is most probably because the minimum nest entrance diameter is likely to be constrained by a bird’s body size (Walankiewic *et al*. 2007), and there is little difference in body size between these two species (del Hoyo *et al*. 2006, Töpfer 2006). Collias and Collias (1984) stated that the size of the inner nest cup is automatically molded to the body size of the parent bird because of the movements involved during nest building. There are no differences in nest cup depth between Narcissus and Green-backed flycatchers (Table 4).

The breeding ecology and natural nests of the Narcissus Flycatcher nesting have been described in detail for the first time. Such details of natural nest sites and breeding ecology are important for biologists studying the behaviour of birds nesting in artificial nest box communities as it may help them place their observations within a natural context. It is hoped that this paper may facilitate the further study of the biology, ecology, life history, and other aspects of the natural history of the Narcissus Flycatcher and other secondary cavity nesters.

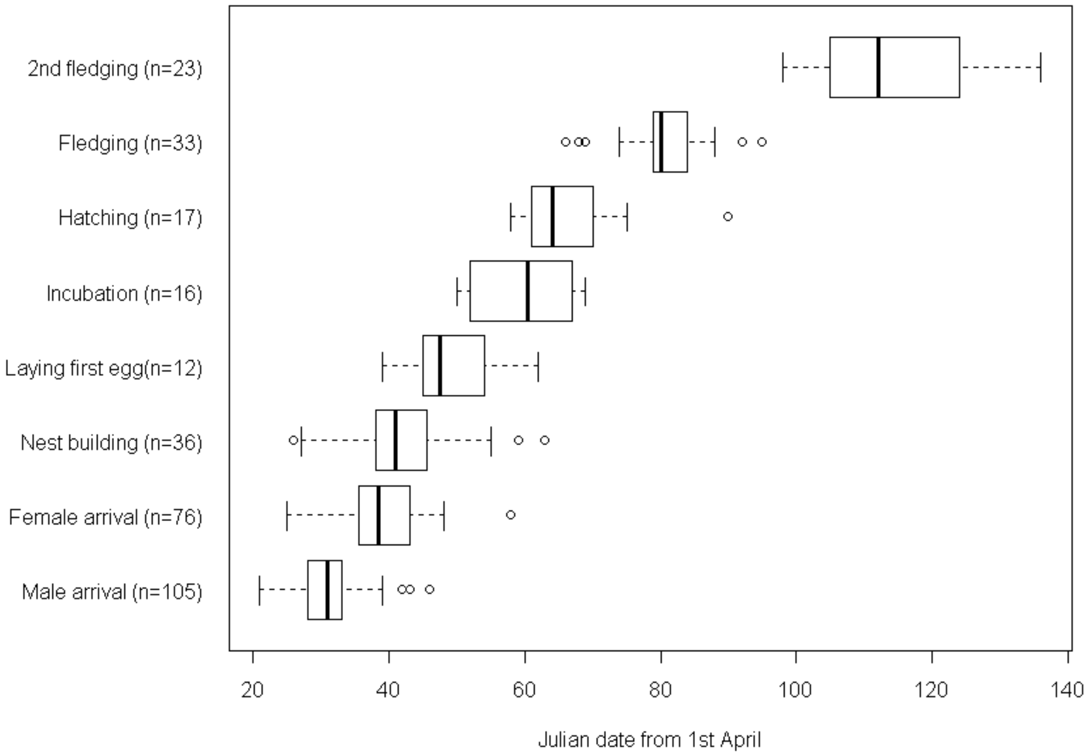


Figure 1. Breeding seasonality of the Narcissus Flycatcher on Mt Fuji, Japan. n indicates the number of observations.

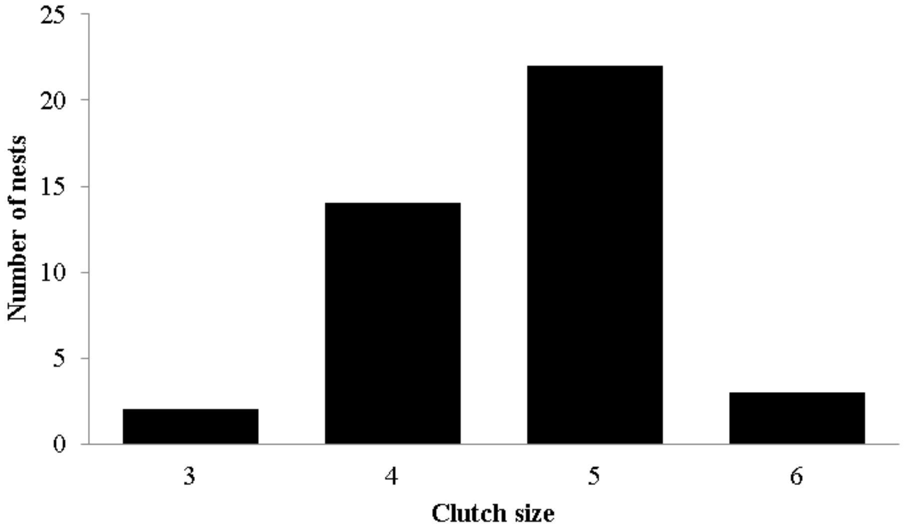


Figure 2. Clutch size of the Narcissus Flycatcher.

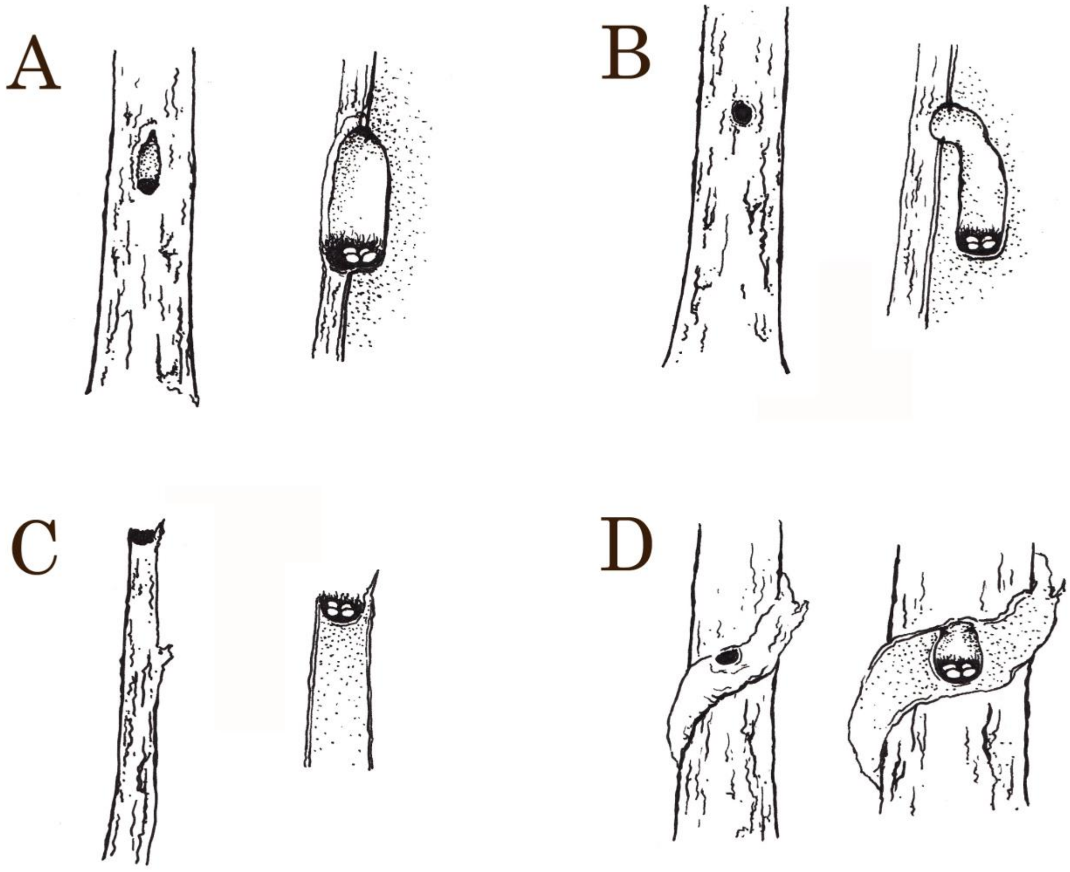


Figure. 3. Nest Types: A half cavity (shallow cavity with a wide entrance); B full cavity (deep cavity with narrow entrance); C chimney (usually in broken and rotten top of thin tree); D shelf (outside the main trunk, usually in a vine).

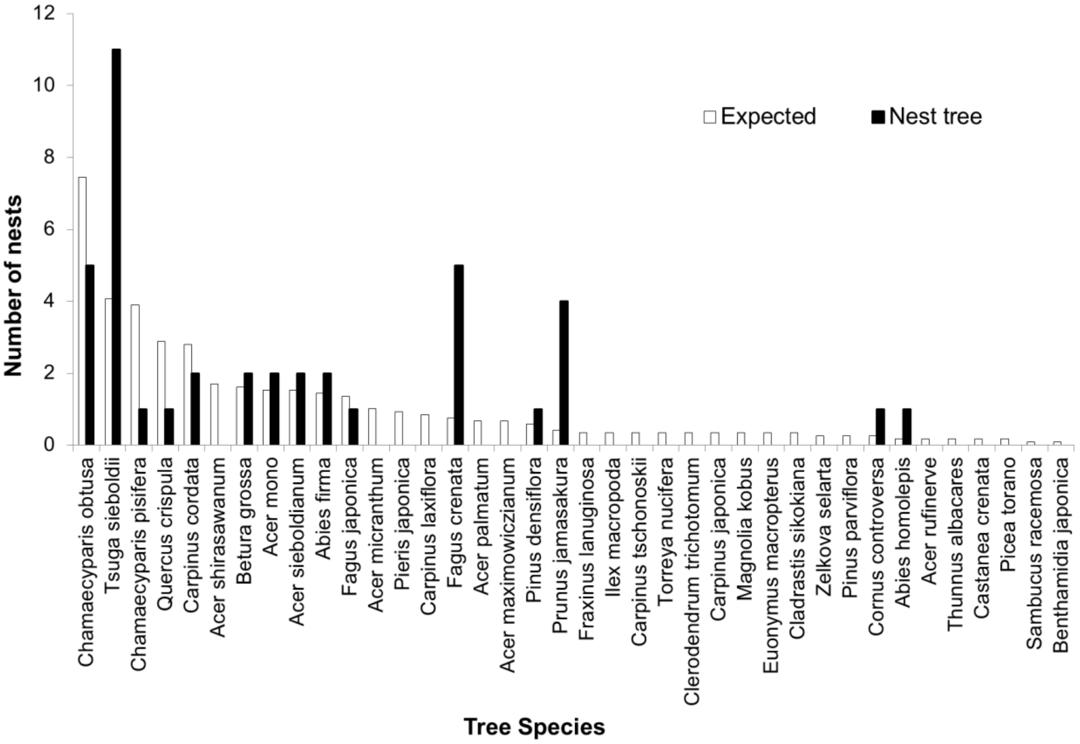


Figure. 4. Nesting tree species preferences of Narcissus Flycatcher: a) deciduous broadleaf forest, b) evergreen coniferous forest.

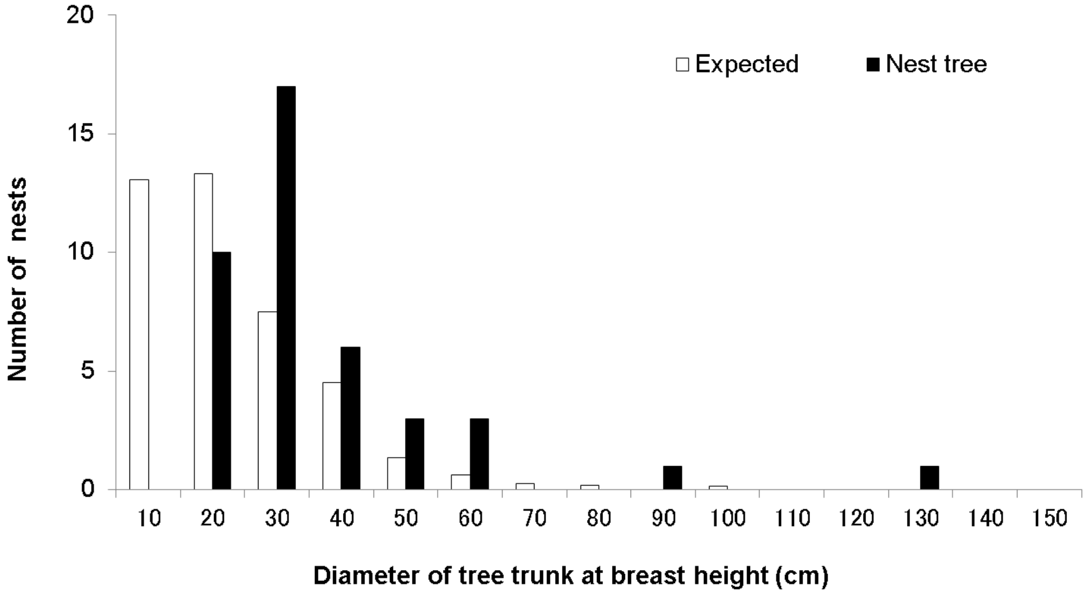


Figure. 5. The DBH of Narcissus Flycatcher nesting trees.

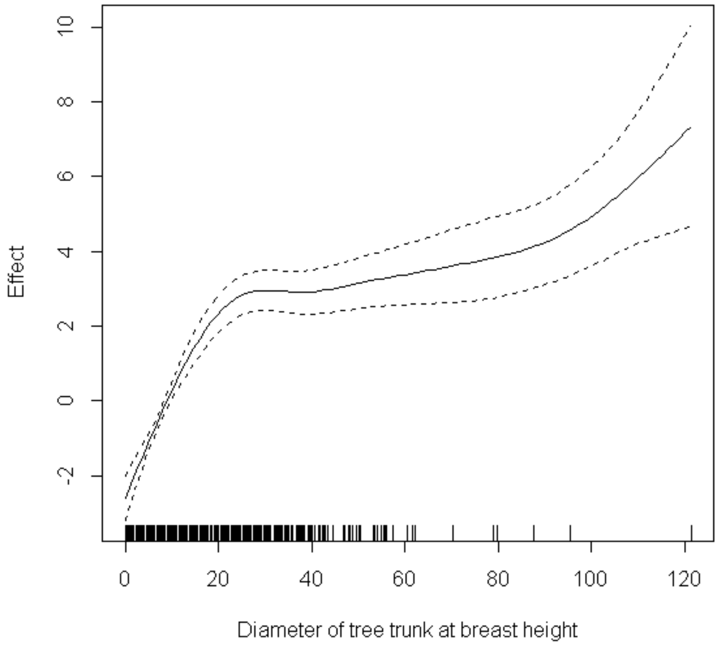


Figure. 6. Fixed effect of DBH on nest site preferences of Narcissus Flycatcher in GAMM. The line shows an estimated equation generated by generalized additive model and two sided 95% confidence intervals. | on the x axis indicates that data exists.

Figure. 7. Actual and expected use of dead and live trees.

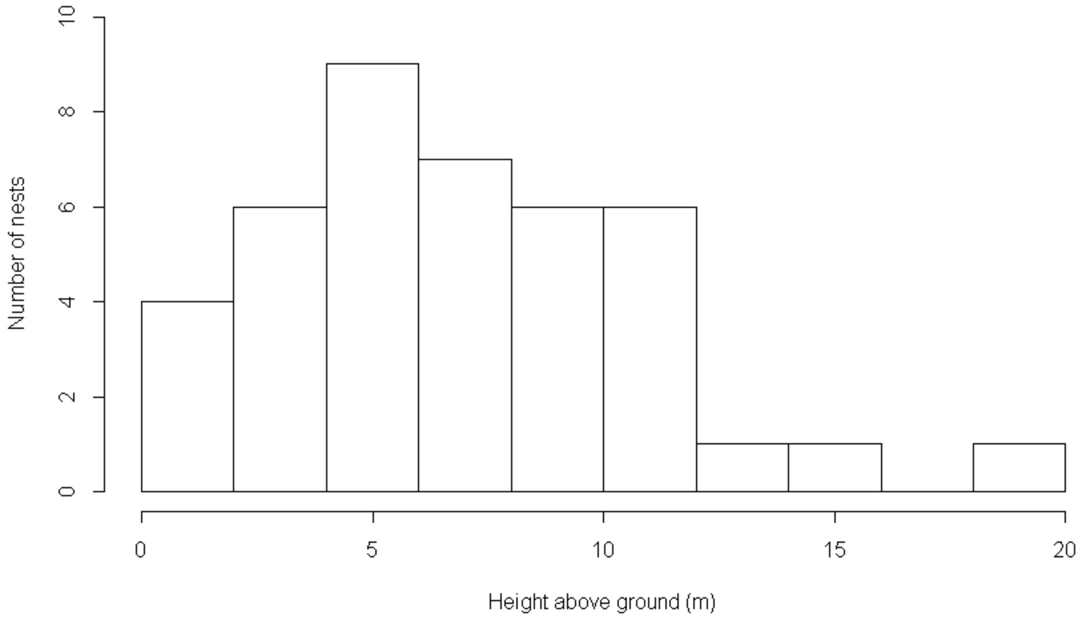


Figure. 8. The height above ground of Narcissus Flycatcher nests.

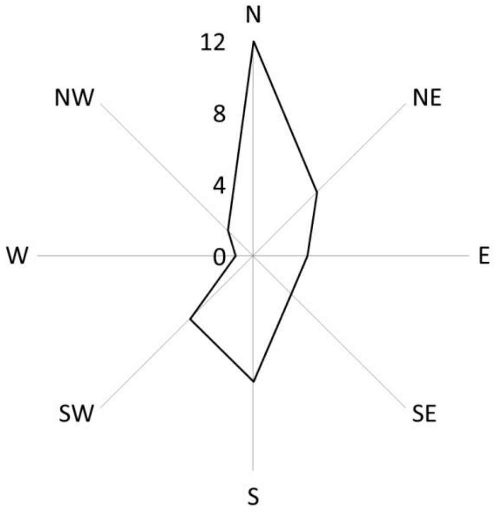


Figure. 9. Nest entrance orientation. Solid lines indicate numbers of observations.

Table 1. Model selection results for generalized additive models of nest site preference by Narcissus Flycatchers. Only models ΔAIC<2 and Null model are listed.

Variables	logLik	AIC	ΔAIC
Diameter of tree trunk, Dead or live	-126.8	263.50	0.00
Null	-173.7	351.30	87.80

Table 2. Best model describing the nest site preferences of the Narcissus Flycatcher.

Fixed effects	Estimate	SE	z	P
(Intercept)	-5.44	0.57	-9.48	<0.01
Condition of tree (Dead tree)	2.08	0.37	5.59	<0.01
s(DBH)	2.95	1.06	2.78	<0.01

Table 3. Breeding ecology of *Ficedula* flycatchers

Species	Scientific name	Migration status	Breeding latitude [a]	Social system	Clutch size	Death by starvation (%)	Nest building (days)	Incubation period (days)	Nestling period (days)	Feeding fledgling (days)	References
Narcissus Flycatcher	*F. narcissina*	Migrant	35°N	monogamy	3–6	0	2–10	10–13	10–12	19 at maximum	this study
Green-backed Flycatcher	*F. elisae*	Migrant	40°N	monogamy	3–6	0		12–14	12–14		Wang *et al.* 2008
Yellow-rumped Flycatcher	*F. zanthopygia*	Migrant	41°N	monogamy	3-9	0	3-4	11-15	11–15		Liu and Wang 1981, Wang *et al*. 2008, Deng *et al*. 2010, Cao *et al*. 2010
Atlas Pied Flycatcher	*F. speculigera*	Migrant	36°N		2-6	0	5-11	12-16	14-18		Boudeffa *et al*. 2014
Semicollared Flycatcher	*F. semitorquata*	Migrant	44°N	mainly monogamy	4-7		5-16	13-14	14-17		Curio 1959, Georgiev and Iankov 2009, del Hoyo *et al*. 2006
Collared Flycatcher	*F. albicollis*	Migrant	49°N	polygyny 9-92%	2-10	2–38	few days	12–20	14–18	6-14	del Hoyo *et al*. 2006, Gustafsson and Qvarnström 2006, Sendecka 2007, de Heij *et al*. 2011
Red-breasted Flycatcher	*F. parva*	Migrant	56°N	mainly monogamy	4–7	0	3–5	12–15	11–15	8–10	Mitrus 2006, Mitrus and Soćko 2004, 2005, 2008, del Hoyo *et al.* 2006
Pied Flycatcher	*F. hypoleuca*	Migrant	60°N	monogamy 40%, polygyny 60%	3–10	20-26	4–11	13–16	11–18	about 7	Lundberg and Alatalo 1992, del Hoyo *et al.* 2006

[a] the breeding latitude was estimated by the breeding distributions (del Hoyo *et al*. 2011)

Table 4. Natural nest characteristics of Narcissus *F. n. narcissina* and Green-backed *F. elisae* flycatchers. Numbers indicate the mean±SD.

		Narcissus flycatcher *F. n. narcissina* this study n=41	Green-backed flycatcher *F. n. elisae* Wang *et al.* (2007) n=34
Nest site	Types of nest sites	Full cavity, Half cavity, Chimney , Shelf	Branch junction, Cavity, Chimney
	Nest height (m)	7.3 ±4.1	2.3±0.4
	Rate of nesting dead fragment	51%	60%
	Diameter of tree trunk at breast height (cm)	30.9± 20.8	16.0± 2.4
Entrance	Greatest diameter (cm)	26.4 ± 45.6	17.7± 6.2
	Smallest diameter (cm)	7.4 ± 2.2	6.8± 0.5
Nest Hole	Greatest diameter (cm)	9.9 ± 1.4	8.6± 0.6
	Smallest diameter (cm)	8.3 ± 1.3	
	Hole depth (cm)	7.0 ± 4.2	11.7 ± 4.2
Nest	Inner diameter (cm)	6.5 ± 0.4	5.3 ± 0.1
	Nest depth (cm)	3.2 ± 0.7	3.4 ± 0.1
	Nesting materials	Dead leaves, Moss, Fiber of plant, Animal hear	Dead leaves, Moss, Fiber of plant, Animal hear

Chapter II

Male Morphology and its variation

Age determination is one of the principal information for ornithology and behavioural ecology. In most of European passerines, the age determination methods were already elucidated. Plumage color, feather worn, moulting, shape of feathers, iris color, skull ossification and also the measurement is useful to age determination but there is wide difference among species (Svensson 1992). On contrary, there is only a few information of age determination of bird in East Asia; furthermore most of bird species have not studied yet.

The Narcissus Flycatcher has sharp sexual dimorphism on plumage color (Yamashina 1941). In addition, yearlings of both sexes usually sustain the juvenile feathers on the greater coverts and the flight feathers (Yamashina 1941). Thus at least I can easily determine the yearlings and the sex of individuals in breeding seasons (Fig. 1). It is known that the other subspecies of the flycatcher *F. n. owstoni* takes over 3years to become a full adult plumage (Kuroda 1925), and I can possibly determine the 2nd winter plumage the nominotypical subspecies, *F. n. narcissina* (Yamashina 1941).

In this study, I follow the individual breeding among 5years and follow the plumage color change. It makes us possible to clarify the real age of the individuals and then I compared the morphological difference (measurements, plumage, and iris color) of 1st, 2nd, and older individuals.

METHODS

I studied in the breeding season of Narcissus Flycatcher from April to June in 2010-2011 on the study site in the Fuji primitive forest (35°27′N, 138°38′E, 1140 m). Males are captured with the mist net and the wing length, tail length were measured. In addition, I determine the moulting status of the flight feathers, tibial feather, and iris color. Natural wing length was measured with digital caliper (Mitsutoyo, accuracy is 0.1 mm Svensson 1997). The tail length was measured with wing measure (accuracy is 0.5 mm Svensson 1997). I recorded the colour of the each feather and greater coverts (brown juvenile feather or adult type pure black). I also classify the color of tibial feather (pale brown, gray black, and pure black), the feather density and worn. I classified the iris color (greyish brown, brown, and reddish brown), with the exact same light electrical torch.

The first summer individuals are determined the sustaining brown juvenile feather in some part of body, and 2nd summer individuals are the individuals had captured in prior year and classified as yearling. The older individuals are adults which had been captured prior seasons as adult individuals. In the analysis I used R 2.12.2 (R development core team 2011).

RESULTS

In the study periods, I captured 14 yearlings, 7 second summer individuals, and 8 old males. The natural wing length of yearlings was significantly shorter than older individuals (1st summer 74.70±1.03 mm (SD), second summer 77.70±1.58 mm(SD), third summer or older 76.54±1.50mm (SD), Fig. 1, Turkey’s test, yearlings vs second summer plumage $P<0.01$, yearlings vs older than second summer plumage $P < 0.01$, yearlings vs older than second summer plumage $P<0.01$). On the other hand there is no difference between the 2nd summer and older (Fig. 1, Turkey’s test, 2nd summer plumage vs older than second summer plumage $P=0.18$). The measurements are overlapped among age groups. All yearlings sustained the juvenile feathers on the flight feathers. There was also significant difference of tail length among age groups, (1st summer 50.65±1.37 mm (SD), second summer 51.93±1.13 mm(SD), third summer or older 52.00±1.15 mm(SD), Fig. 1, Turkey's test, yearlings vs second summer plumage $P < 0.05$, yearlings vs older than second summer plumage $P < 0.01$, second summer plumage vs older $P=0.99$). Two yearlings sustained the brown feather on tail, but others had pure black tail. The color of tibial feather were significantly different (Table 1, Fig.2, Kruskal-Wallis test, $P<0.01$). Tibial feather color changed with age. First summer plumage was all light brown feathers; while a small number of grayish black feathers appeared during the 2nd summer. Birds of 3rd summer or older showed a dense covering of pure black feathers.

Iris color was also different with age; from grayish brown in the 1st summer, to brown in the 2nd summer, to reddish brown in the 3rd summer and afterwards (Table 2, Fig.3, Kruskal-Wallis test, $P<0.01$). These results show that both tibial feathers and iris color are useful traits for determining the age of male Narcissus Flycatcher.

DISCUSSION

Here I figured out the Narcissus Flycatcher takes 3 years to become full adult. Commonly the natural wing length of juvenile is shorter than adult (Svensson 1992 , Perez-Tris and Telleria 2001). All yearlings having juvenile primaries thus the difference caused by the difference of juvenile feather and adult's. On the other hand there was no difference among 2nd summer plumage and the older. This result indicate the measurement is meaningless to determine the older males.

The color of tibial was significantly different among age classes. Tibial feather color has previously used to determine age of the Great-tailed Grackle *Quiscalus mexicanus* (Phillips 1950), and to determine the species of genus *Topaza* and *Quiscalus* (Phillips 1950, Hu et al. 2000). From this study it is useful to determine the age class of Narcissus Flycatcher. Only few studies treat the morphology of tibial feather, but there can be some other species also changing the tibial color with age. The iris color change is common phenomena of birds (Svensson 1992). Same as our result, for instance, the iris color of reed warbler *Acrocephalus scirpaceus* change with age. I figured out the iris color change of Narcissus Flycatcher, but in some cases the older male didn’t have reddish iris. It suggests the iris color change takes many years or there is the individual difference. In conclusion, our study suggest I can classify the age of Narcissus Flycatcher in three groups. This basic information can accelerate the future study of Narcissus Flycatcher.

Table 1. Changes in color of Tibial feathers with advancing age.

	Pale brown	Pale Black	Black
1st Summer plumage	14	0	0
2nd Summer plumage	0	8	0
Full grown (3S+)	0	0	7

Table 2. Changes in Iris color with advancing age.

	Greyish Brown	Brown	Reddish Brown
1st Summer plumage	14	0	0
2nd Summer plumage	0	6	0
Full grown (3S+)	0	2	4

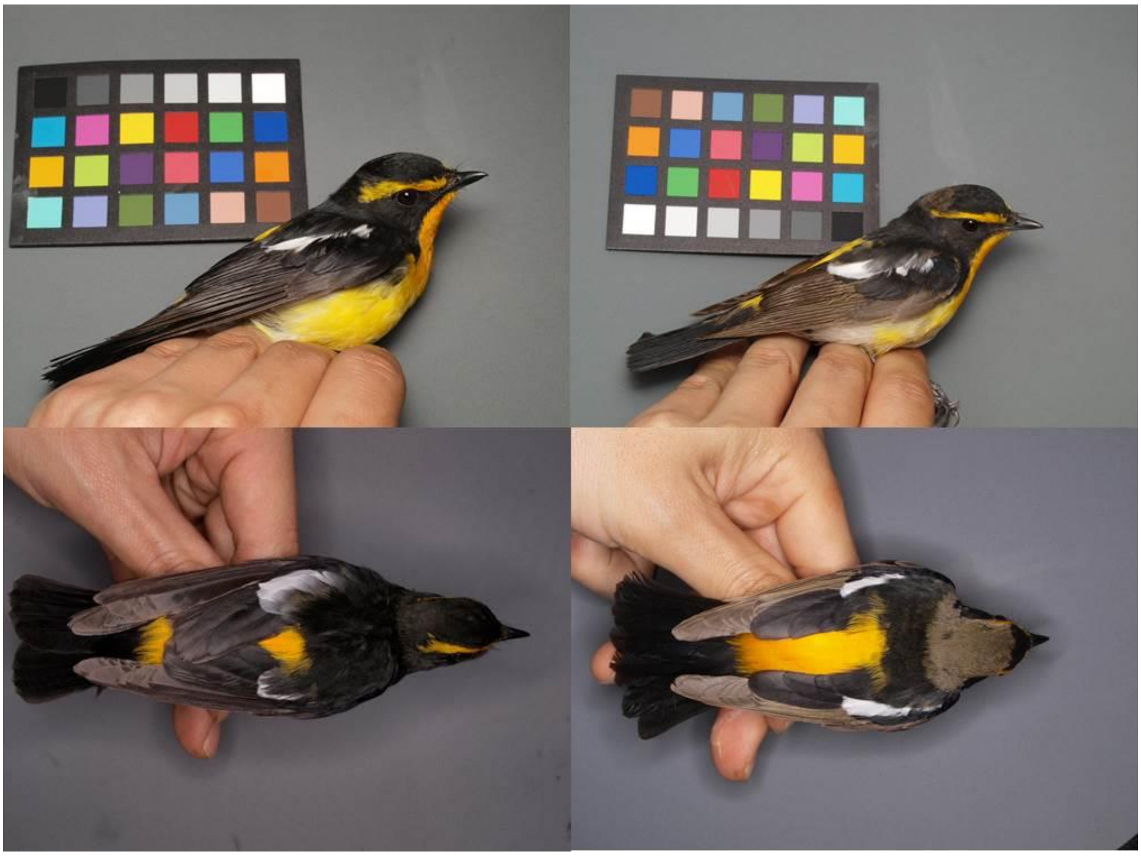


Figure 1. Difference of plumage color of matured (left) and yearling (right) male. Yearling has brown juvenile feather on the wing and back head.

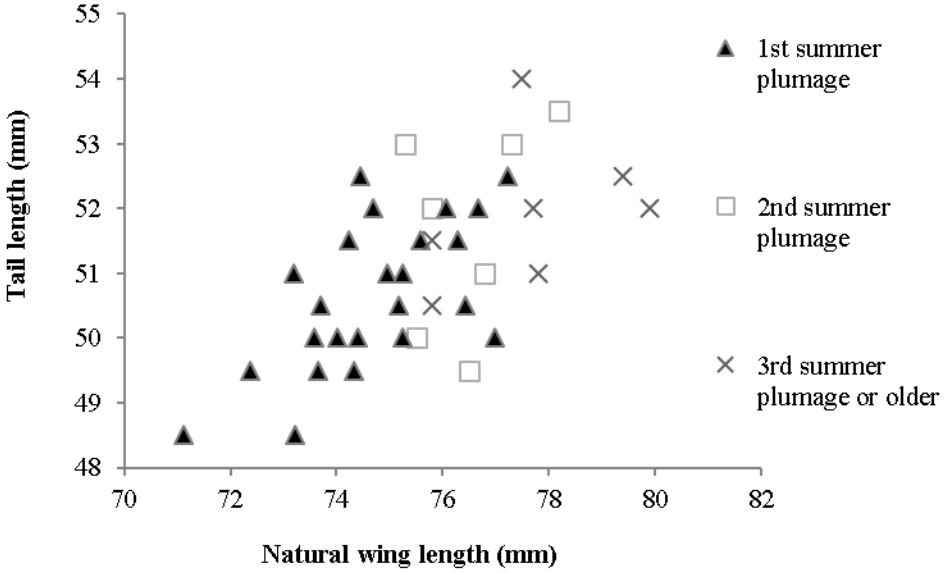


Figure 2. Wing and tail lengths of *Ficedula narcissina*.

Figure 3. Tail color of matured (left) and yearling (right)

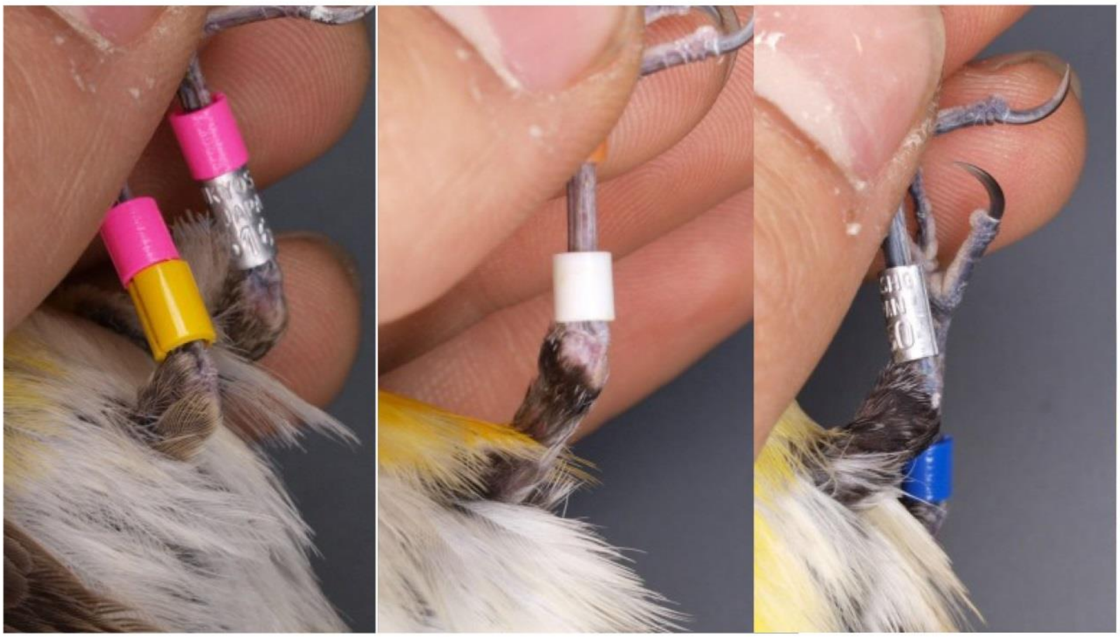


Figure 4. Tibial feathers: 1st summer plumage (left), 2nd summer plumage (center), and 3rd summer or older (right).

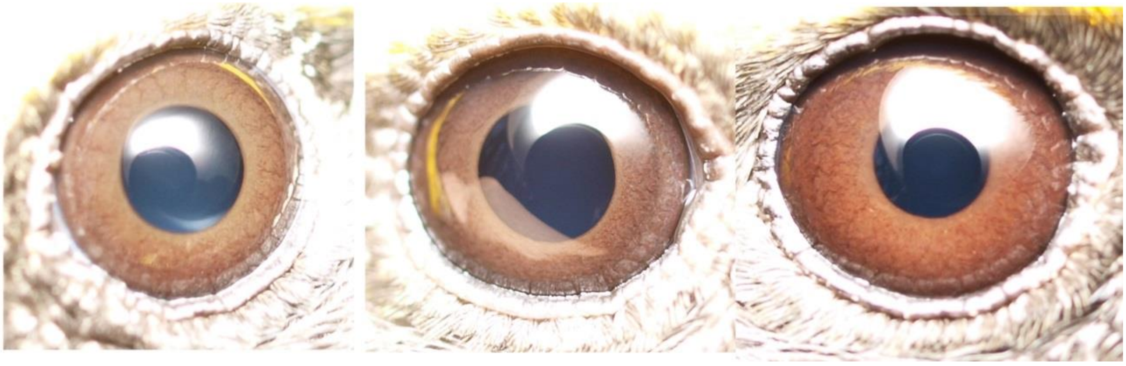


Figure 5. Iris colour change with age: 1st summer plumage (left), 2nd summer plumage (center), and 3rd summer or older (right).

Chapter III

Carotenoid-based and depigmented patches on Narcissus Flycatcher *Ficedula narcissina* convey different time scale condition

Many birds have multiple ornaments (Møller and Pomiankowsky 1993, Johnstone 1996, Guindre-Parker and Love 2013), for example, different plumage colourations (i.e. melanin, carotenoid, structural colour, and depigmented white; Hill and MacGraw 2006, Stoddard and Prum 2011), several ornaments constructed with the same pigmentation (Badyaev et al. 2001, Pryke et al. 2002, Guindre-Parker et al. 2013, Boves et al. 2014), and the combination of plumage colouration and length (Andersson 2002). In different contexts, such multiple ornamentations might signal different male quality for sexual selection (Multiple message hypothesis; Møller and Pomiankowski 1993, Johnstone 1996, Török et al. 2003, Hegyi et al. 2010), or they might be redundant signals for females (Back up signal hypothesis; Møller and Pomiankowsky 1993, Johnstone 1996, Candolin 2003). The multiple message hypothesis states that multiple ornaments may be maintained simultaneously when each ornament is indicative for a different aspect of male quality (i.e. genetics, feeding ability, or resource holding power). In contrast, the redundant signal hypothesis states that although each signal conveys the same information such as overall-male quality, the redundant signals enhance the precision and reliability of mate choice (Møller and Pomiankowski 1993, Candolin 2003, Loyau 2005). Increasing numbers of studies attempted to determine the function of multiple ornaments on birds (i.e. Jennions and Petrie 1997, Freeman-Gallant et al. 2010, Taff et al. 2013). However the benefits and developmental trade-offs of multiple ornaments are still complex because the production of indicator traits is affected by many physiological processes with varying degrees of condition dependence (Badyaev et al. 2001, Leskinen et al. 2012, Guindre-Parker and Love 2013). Moreover, the advantages and developmental trade-offs may change with age (Boves et al. 2014, Grunst et al. 2014) and environment (Alatalo et al. 1986, Lifjeld and Slagsvold 1988, Taff et al. 2013). Thus, knowledge of developmental and functional interrelationships among the components of a condition-dependent trait is essential for understanding the evolutionary changes in the trait (Endler 1992, Badyaev and Hill 2001, Guindre-Parker and Love 2013).

Plumage colours are developed during specific moulting periods and hence reflect the nutritional status at the time of the moult (Hill and McGraw 2006, de la Hera et al. 2010. Grindstaff et al. 2012). Moulting seasonality differs among bird species and populations (Ginn and Melville 1983, Svensson 1992, Barta et al. 2008, Newton 2009). Some migratory birds have two moulting periods. One is a partial pre-breeding moult in the wintering area, and the other is a complete post-breeding moult in the breeding area (Ginn and Melville 1983, Barta et al. 2008, Newton 2009). Breeding plumages of these species bear patches of feathers constructed in the wintering area and some produced in the breeding area (Svensson 1992). Therefore, plumages that develop in different areas may indicate the condition of individuals during different periods. If an individual's condition is stable, and there is a correlation between plumage colourations of the pre-breeding moult and those of the post-breeding moult, the two different plumages can be work as redundant signals to convey the condition of the individual throughout the year. However, if there is no correlation between these two plumage colourations, the two different plumages can show different aspects of male quality. In addition, the moulting seasonality of some migratory birds differs between mature and immature. For example, yearlings should wear mature-male-like plumage to bear sexual traits in the partial pre-breeding moult; however, mature male does not have to moult excessively to show this. Thus, even if the breeding moults of a yearling and mature male look similar, the basic message of the plumages might be different. It is crucial to determine the correlations among multiple morphological traits within age classes in order to reveal the role of multiple traits in birds.

The Narcissus Flycatcher *Ficedula narcissina* is a sexually dimorphic, small, migratory passerine, breeding in Northeast Asia and wintering in Southeast Asia (del Hoyo et al. 2006, Töpfer 2006). It is socially monogamous; nests in wood cavities and both parents care for nestlings and fledglings (Nakamura and Nakamura 1995, Okahisa *et al*. 2012). The male Narcissus Flycatcher has bright yellow carotenoid-based patches on the breast and rump, and depigmented wing patches on the wings (mainly on the inner greater and medium coverts, and in some cases also on the tertials). In addition, the summer plumage colourations of yearling males differ significantly from those of mature males. The entire upper part of a mature male is jet black. On the other hand, the primaries, secondaries, tertials, greater coverts, medium coverts, lesser coverts, and alula of yearling males have some female-like, brown juvenile feathers, and the number of brown feathers they have varies (Yamashina 1941, Okahisa *et al*. 2013). First-winter males moult body feathers (including forehead, breast, rump and all under parts), coverts, tertials (including inner secondaries in a few cases), and tails (all or partial). They bear sexual traits (black upper parts, yellow breast and rump patches, and white wing patches) during the pre-breeding moult in the wintering area. In contrast, mature males have a complete post-breeding moult in the breeding area, mainly in July or August. They also have a partial pre-breeding moult of some body feathers (including the breast), a few coverts, and the tail feathers (all or partial) in the wintering area (Yamashina 1941). In addition, older individuals have a more reddish iris colour, and darker and denser tibial feathers (Okahisa *et al.* 2011).

In this study, the carotenoid-yellow patches on the breast and the rump, and the depigmented white patches of male Narcissus Flycatchers were focused. Males display their breast plumage to females to attract them for pairing by raising their heads and shaking them slowly and smoothly. In addition, males flush their plumage colourations in display flights to attract mates. They also strongly attack the body plumage in male-male competitions. Thus, these plumage colourations may play an important role in the sexual selection. Carotenoid-based colourations are recognized as an important signal, yet the essential mechanisms that maintain their honesty is not well understood (Hadfield and Owens 2006). Animals can only obtain carotenoids from their diet (Goodwin 1984). The amount deposited in ornaments reflect the individual’s ability to acquire and assimilate these pigments (Peters et al. 2008). In addition, the message of the depigmented white patches of the Ficedula flycatcher is not well understood (see Török 2003). It can weakly reflect the prior condition of individuals (Török 2003) but is usually treated as a sexual trait indicating genetic quality (Potti 1993, Sheldon et al. 1997, Sheldon and Ellegren 1999, Sanz 2001, Sirkiä and Laaksonen 2009, de Heij et al. 2011, Laczi et al. 2011). To reveal the benefits and developmental trade-offs of such multiple traits, the degree of conditional dependence, while considering both age and environment were tested.

The aims of this study are to (1) reveal the changes in the colouration of the carotenoid patches and the size of the depigmented white patches with age, (2) determine correlations between multiple traits, (3) examine the effects of territory quality on the colours of the plumage that develop in post-breeding moulting, and (4) determine whether these multiple traits reveal multiple messages conveying different condition dependencies or redundant signals.

METHODS

Field research

Data were collected from 15 April to 15 June in 2010, 2011, 2012, and 2013, during the breeding season of the Narcissus Flycatcher, in Fuji Primitive Forest, Central Japan (35°27′N, 138°38′E; 60 ha; 1140 m above sea level). The study area consists of two forest types: deciduous broadleaf forest and evergreen coniferous forest. The deciduous broadleaf forests are dominated by old growth Japanese Oak (*Quercus crispula*), Siebold's Beech (*Fagus crenata*), and Japanese Blue Beech (*F. japonica*). The evergreen coniferous forests are dominated by old growth Japanese Cypress (*Chamaecyparis obtusa*) and Japanese Hemlock (*Tsuga sieboldii*) (Okahisa et al. 2012). Arthropods (Diptera, Lepidoptera, Hymenoptera, and Coleoptera) are more abundant in the broadleaf forest than the coniferous forest (Okahisa et al. in press), and the Narcissus Flycatcher in the broadleaf forest had larger clutch sizes than those in the coniferous forest (Yuji Okahisa submitting).

Each male was lured into a mist net using song playback within his territory or at a rain puddle. The age of each bird was determined by plumage characteristics (Okahisa et al. 2013). Males were uniquely ringed with a combination of aluminium (authorized by the Japan Environment Agency) and colour-coded rings. The following measurements were taken: body mass with a 30 g Pesola spring balance (to the nearest 0.1 g, Pesola AG, Rebmattli, Baar, Switzerland), wing length with Mitsutoyo sliding digital callipers (natural wing chord in 0.1 mm, Mitsutoyo Corp., Kawasaki, Kanagawa, Japan), and tarsus length with Mitsutoyo sliding digital callipers (to the nearest 0.1 mm). The moulting status (feathers moulted in the wintering area or brown juvenile) of each greater covert, primary, secondary, tertiary, and rectrices were recorded. The sum of the moulted feathers on these parts was used as an indicator of the moulting status of an individual.

Singing males were searched in the study area every morning (03:30–11:30). When a singing male was observed, the male was followed and plotted the singing location on maps. The locations of singing points were plotted using the colour markings on trees every 20 m (made before the spring migration of Narcissus Flycatchers), and each marking was located with a GPS (Garmin, eTrex Legend, accuracy was ± 8 m). One observation trial was just 5 minutes, and the trial was repeated every day. Finally, the minimum convex polygon of their song locations was calculated with ArcGIS 10.1 (Environmental Systems Research Institute). It was considered as a flycatcher's territory. To estimate the territory quality of the individual, the vegetation characteristics of the habitats were described in 50 randomly placed 10 m × 10 m quadrats in each forest type (deciduous broadleaf and coniferous evergreen). The number of each tree species and their diameter at breast height (DBH) values were recorded for each quadrat. Next, the area-weighted average proportion of broadleaf trees of each territory was calculated with ArcGIS. It is known that this proportion of broadleaf forest is a suitable explanatory factor for predicting prey abundance for the insectivorous birds in the study area (Okahisa et al. in press).

Colour analysis

Upon the capture, five breast feathers, five rump feathers, and three feathers of greater coverts were plucked from males for spectrometric analyses. The feathers were placed on the black background to follow the natural situation (Bentz 2013). The measurements of plumage colouration were obtained at the beginning of breeding. The spectral reflectance between 300 and 700 nm was measured using an Ocean Optics Jazz spectrometer (range 200–800 nm, Ocean Optics Inc., Dunedin, FL, USA), illuminated with both UV (deuterium tungsten-halogen bulb) and visible (tungsten-halogen bulb) light sources, and a WS-1 white standard (Ocean Optics Inc., Dunedin, FL, USA). A bifurcated micron fibre optic probe was used at a 90° angle, 1 mm from the feather's surface (Bentz 2013).

For the analysis of reflectance, I used AVICOL software (Gomez 2006). Initially, I summarized the reflectance data (Fig. 1). To compare the entire colour pattern of the bird, I also used the model of Endler and Mielke (Endler and Mielke 2005) following (Peters et al. 2008). For each reflectance plumage patch, I determined cone quantum catches based on spectral sensitivities of the four cones (VS: very short, S: short, M: medium, and L: long wavelength sensitive cones) used in the colour vision (Endler and Mielke 2005, Peter 2008). The sensitivity of the cone type was based on cone sensitivities for type U-eyes according to Appendix A in Endler and Mielke (2005). I then divided each cone quantum catch by the sum of all four and transformed these according to Kelber et al. (2003), to obtain three independent relative cone catches—x, y, and z—according to this transformation. Higher values of x represent greater stimulation of the L cone and lower stimulation of the M cone; higher y values represent greater stimulation of the S cone, and higher values of z greater stimulation of the VS cone (Endler and Mielke 2005, Peters et al. 2008). These relative cone catches can be represented as points in the tetrahedral avian visual space. I calculated the first principal component (PCxyz, Peters et al. 2008), which explained 78–94% of the each variation (Table 1). I also determined the white patch on the wing by scoring the size of the white patch on each feather from the greater coverts and tertials (Fig. 2). The greater coverts and tertials overlap each other and move easily. It makes calculation of the real total area difficult. Thus the sum of each wing patch size was used as an indicator of whole white patch size.

Statistical analysis

All statistical tests were carried out using R version 3.0.0. (R development core team 2013). To examine the difference in male morphology based on the age and study year, linear mixed models (LMMs) with Gaussian error and the identity link function were used. Linear models (LMs) were also used for testing these effects on wing patch reflectance. P-values for age and study years were obtained from a likelihood F-test. The male age used as a rank variable, but the study years were used as a factor variable. To test correlations among male characteristics and morphological repeatability of breast plumage colour, Pearson's correlation test and Spearman's rank correlation test were used. The morphological characteristics to the previous and present year were compared in the test of morphological repeatability. The LMMs with Gaussian error and the identity link function was also used for testing the effects of prior territory on morphological characteristics in the next year. In this case, the proportion of broadleaf tree was included as an explanatory variable. Study year and IDs of individuals were used as random factors. To test the effects of morphological change, characteristics in the year (t) – the trait in the year (t – 1) was used to determine the difference in a given morphological trait.

RESULTS

No differences in breast, rump, and wing patch reflectance among the age groups were found (Table 2), but the wing patch size significantly increased with age. The breast reflectance was different among the study years. The carotenoid-based pigmental breast and rump reflection were not correlated with each other in mature males or yearlings (Fig. 3, Pearson's correlation test: breast and rump in mature male, t = 1.53, df = 69, P = 0.13; breast and rump in yearling, t = 0.96, df = 57, P = 0.34). In addition, no correlation was found between the depigmented wing patch reflections and the patch size (Spearman’s rank correlation test: wing patch reflectance and wing patch size in mature males S = 122.10, P = 0.95; wing patch reflectance and wing patch size in yearling S = 21.19, P = 0.50).

No correlations were found between other morphological traits (Pearson’s correlation test: wing patch reflectance and breast in mature males t = -0.21, d = 9, P = 0.84; in yearlings, t = 0.14, df = 6, P = 0.89; wing patch reflectance and rump in mature males, t = 1.25, df = 8, P = 0.25; in yearlings, t = 2.36, df = 6, P = 0.06; Spearman’s rank correlation test: wing patch size and breast plumage; yearlings, S = 18168.81, P = 0.93; mature males, S = 30190.76, P = 0.82; wing patch size and rump plumage; yearlings, S = 16165.05, P = 0.15; mature males, S = 23705.41, P = 0.34).

Wing patch size change had strong repeatability (Spearman’s rank correlation test, rho = 0.67, S = 592.05, P = 0.00097) but I found no other repeatability in plumage reflections (Pearson’s correlation test: breast reflection, t = 0.50, df = 15, P = 0.62; rump reflection, t = 0.41, df = 15, P = 0.69). Comparing the morphological characteristics in the year (t) and year (t + 1), the rump reflectance component of 2-year-old males significantly increased when they had occupied a territory with more broadleaf trees in the past year (Table 3, Fig. 4). This tendency was not found in mature males. The rump reflectance component indicates higher values of the L cone and lower stimulation of the M cone, greater stimulation of the S cone, and lower stimulation of the VS cone. In other words, the rump plumage of 2-year-old males became coloured with the strongest UV reflection in broadleaf forest areas. While, the proportion of broadleaf tree in the territories did not solely explain white patch size on the flycatcher in the past year, but longitudinal change in wing patch size was significantly correlated with previous territory. The wing patches became large when individuals had occupied the territory in broadleaf dominant area (Table 4, Fig. 4). No effects of territory on breast reflectance and its change were found.

DISCUSSION

Carotenoid-based colour indicates parental ability, foraging ability, and their own health (Hill and Montgomerie 1994, Linville and Breitwisch 1997, Olson and Owens 1998, Navara and Hill 2003), because birds must digest more carotenoids in order to bear blighter carotenoid-based ornamentations. The colouration of the rump feathers was correlated with territory quality in the previous year, but no correlation was found between age and other morphological characteristics. It suggests that the yellow colouration of the rump signal an individuals' condition in the previous post-nuptial season. Interestingly, the rump colour in 2-year-old males was correlated with the previous territory quality. However, no correlation was found in old males. This result suggests that older males compensate for territory quality and obtain food equally well in the broadleaf forest and the coniferous forest. Grunst et al. (Grunst et al. 2013, see also Badaev and Duckworth 2003) argued that the association between the condition and carotenoid-ornamentation might decline with age because the carotenoid saturation with age masks the effect of condition on ornamentation (Copeland and Fedorka 2012). The results of rump plumage might support this argument. A correlation was found only in the first post-nuptial moulting of sub-adults. Thus, the rump feathers could be differently reliable in conveying individual condition in different age groups.

In contrast, the breast carotenoid-based pigmentation was correlated with neither age nor previous territory quality. This is probably because the Narcissus Flycatcher moults its breast feathers in the wintering area. If the social ranks in breeding area were correlated with those in wintering area, the breast and rump plumage colouration should have been correlated. However, no correlation was found between breast and rump colouration. The results suggest that the carotenoid-based patches on the breast and rump have different messages. The breast colouration might indicate the condition in the wintering area while the rump colouration conveys condition in the breeding area.

I hypothesized that there may be different interrelationships among the multiple traits on a bird body because of the different moult seasonality of the yearlings and the mature males. The breast feathers and rump feathers of yearlings are moulted in the wintering area, and both types of feathers are carotenoid-pigmented. If both patches truly reflect the amount of carotenoid-containing food that they took in the wintering area, there should be a correlation; however, no correlations between the characteristics were found in yearlings, nor in mature males. These results suggest that even in the pre-breeding moult of a yearling male, the condition-dependences of the two carotenoid-based patches are different. The reason is not clear. It is possible that yearlings may have two moulting periods in the wintering area, or the mechanism of these two patches is different. McGraw (2006) reviewed carotenoids in bird bodies and divided them into 24 types (i.e. lutein, zeaxanthins, β-carotene, canary xanthophyll, and astaxanthin). A bird uses seven types of carotenoids for its plumage at maximum. The types differ among patches on a single bird, as well as between the sexes and age groups in some bird species (Hudon et al. 1989, Stradi et al. 1998, McGraw 2006). When moulting birds were fed higher lutein and zeaxanthin, they only accumulated more zeaxanthin, but not lutein (MacGraw et al. 2004). The types of carotenoids that Narcissus Flycatchers accumulate in breast and rump feathers is not known. The spectrum is different (Fig. 1);

thus the two carotenoid patches on the flycatcher might respond differently to conditions because of differences in mechanism.

The white patch size of the Narcissus Flycatcher had considerable variation among individuals; however, the white patch size showed high repeatability within individuals. In addition, the patch was slightly larger in older male groups, similar to other Ficedula Flycatchers (Potti 1993, Török 2003, Laczi et al. 2011). Normally, the size of the depigmented patch of Ficedula flycatchers is treated as a sexual trait indicating genetic quality, with a larger white patch influencing extra-pair paternity and mating success (Potti 1993, Sheldon et al. 1997, Sheldon and Ellegren 1999, Sanz 2001, Sirkiä and Laaksonen 2009, de Heij et al. 2011) for increased genetic benefits, such as inheritance of the phenotype for future attractiveness and improved viability (de Heij et al. 2011, Laczi et al. 2011). The high repeatability of white patch size and enlargement with age could support the idea that depigmented patch size is genetically decided; however, a significant tendency was found for the patch size to increase in individuals living in broadleaf forests. This result is similar to the study of the Collared Flycatcher (*Ficedula albicollis*); the wing patch size of the Collared Flycatcher reflects the prior condition and signals viability (Török 2003). Combining these arguments and the results of this study, the wing patch size of the Narcissus Flycatcher might mainly indicate the genetic quality of males (i.e. viability), while the patch size may also slightly convey long-term condition. The condition-dependence and reliability of white pigmentation are still an ongoing issues (Török 2003, Guindre-Parker et al. 2013), because a larger white patch means a smaller melanin-based black part; thus the bearing cost would be smaller than others (Török 2003, Badyaev and Hill 2000). Here, I have shown the effect of the previous condition on the depigmented white patch size. Further studies are required to reveal the mechanism and developmental trade-off of depigmented white patches.

There could be other reasons why the rump reflectance and the wing patch size of the flycatcher were correlated with the proportion of broadleaf tree in the prior territory because the plumage colouration was not measured immediately after post-breeding moulting, but rather during the following spring. In addition, I cannot rule out the possibility that there were individual differences in the amount of partial pre-breeding moult in mature males, similar to that of yearlings (Okahisa et al. 2012). If there were inter-individual differences in the amount of pre-breeding moult in mature males, the correlation between prior territory and plumage colour could be affected by this pre-breeding moult. For example, broadleaf-inhabiting dominant individuals arriving earlier in the wintering area, could spend a longer time undergoing their pre-breeding moult, and might thus be able to bear higher quality feathers (de la Hera et al. 2010, Dawson 2004). However, to our knowledge, such a carry-over effect of post-breeding condition on the winter moulting of birds has not been demonstrated. In addition, the reflectance of breast plumage that was moulted in the wintering area was not correlated with rump reflectance and white patch size. Thus, there might be no effect of individual differences in the amount of partial pre-breeding moult, or the effect may be limited.

The results of this study determined (1) differences in the condition-dependency of the breast, rump, and wing patches on male Narcissus Flycatchers, (2) there was no correlation among multiple traits, and (3) the effects of prior territory quality on plumage colours of feathers that develop during post-breeding moulting. These results have led to the conclusion that these multiple traits are multiple messages depending on different conditions. It is likely that the message of breast feather colouration is from the wintering condition; the rump feather is from the previous breeding condition, and white patch size is mainly age-based (a sign of viability), although white patch size could also weakly signal previous condition in the breeding area. Theoretical models suggest that multiple condition-dependent signals as handicaps are evolutionarily unstable (Schluter and Price 1993, Johnstone 1996, Iwasa and Pomiankowski 1994), but the finding in the flycatcher opposes this. Theoretical re-construction for the evolution of multiple conditional traits in different periods is needed.

Table 1. Principal Component of plumage colour index, x, y, z in the Endler & Mielke model

	Breast			Rump			Greater Coverts		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Standard deviation	1.53	0.77	0.23	1.59	0.65	0.21	1.68	0.43	0.10
Proportion of Variance	0.78	0.20	0.02	0.84	0.14	0.01	0.94	0.06	0.00
Cumulative Proportion	0.78	0.98	1.00	0.84	0.99	1.00	0.94	1.00	1.00
Factor loading (x)	-0.98	0.08	0.18	-0.98	0.13	0.16	0.98	0.17	0.07
Factor loading (y)	-0.88	0.46	-0.13	-0.93	0.35	-0.13	0.98	0.17	-0.07
Factor loading (z)	0.79	0.61	0.08	0.84	0.53	0.04	-0.94	0.35	0.00
Eigen value(x)	-0.64	0.10	0.76	-0.61	0.20	0.76	0.59	0.39	0.71
Eigen value(y)	-0.57	0.60	-0.56	-0.58	0.54	-0.61	0.59	0.40	-0.71
Eigen value(z)	0.51	0.79	0.33	0.53	0.82	0.21	-0.56	0.83	0.00

Table 2. Difference in patch colouration among age groups. F and p were calculated with LMM (random factor = IDs).

	Yearling	2nd year	3rd or older	Age	Year

Traits	Mean±SD	n	Mean±SD	n	Mean±SD	n	F	p	DF	F	p	DF
Breast reflectance	-0.01±1.53	64	-0.11±1.50	27	0.20±1.46	43	0.41	0.52	1, 132	2.40	0.07	3, 129
Rump reflectance	-0.06±1.64	60	-0.03±1.25	24	0.12±1.60	41	0.27	0.60	1,123	1.18	0.32	3, 120
Wing patch reflectance[*1]	0.47±1.21	9	0.06±0.19	2	0.23±1.77	10	0.16	0.70	1, 19	6.09	0.02	1, 18
Wing patch size	2.90±0.64	55	2.95±0.31	24	3.17±0.51	48	5.00	0.03	1,125	0.29	0.83	3, 122

[*1] When testing the difference in white path reflectance among age groups and years, only differences between yearling and individuals older than 3 years, year 2010 and 2012, were tested with LM

Table 3. Results of the F test with LMMs explaining the effect of prior territory on morphological characteristics in the present year

	Broadleaf tree in territory					
	2nd year old			3rd year or older		
	F	P	DF	F	P	DF
Throat reflectance	0.10	0.76	1,13	0.37	0.57	1,13
Rump reflectance	11.25	0.004	1,14	0.42	0.53	1,13
White patch size	0.64	0.44	1,11	0.07	0.79	1,13
Wing chord	0.004	0.94	1,11	0.01	0.94	1,13
Tail length	0.29	0.60	1,11	0.29	0.60	1,12

Table 4. Results of the F test with LMMs explaining the effect of prior territory on changes in morphological characteristics

	Broadleaf tree in territory		
	F	P	DF
Throat reflectance change	0.006	0.94	1,12
Rump reflectance change	0.49	0.50	1,11
White patch size change	5.25	0.04	1,11
Wing chord	0.27	0.61	1,13
Tail length	0.003	0.96	1,12

Fig. 1. Reflectance spectra of plumage (reddish yellow breast patch, yellow back patch and white patch on greater coverts) colour of the Narcissus Flycatcher (*Ficedula narcissina*).

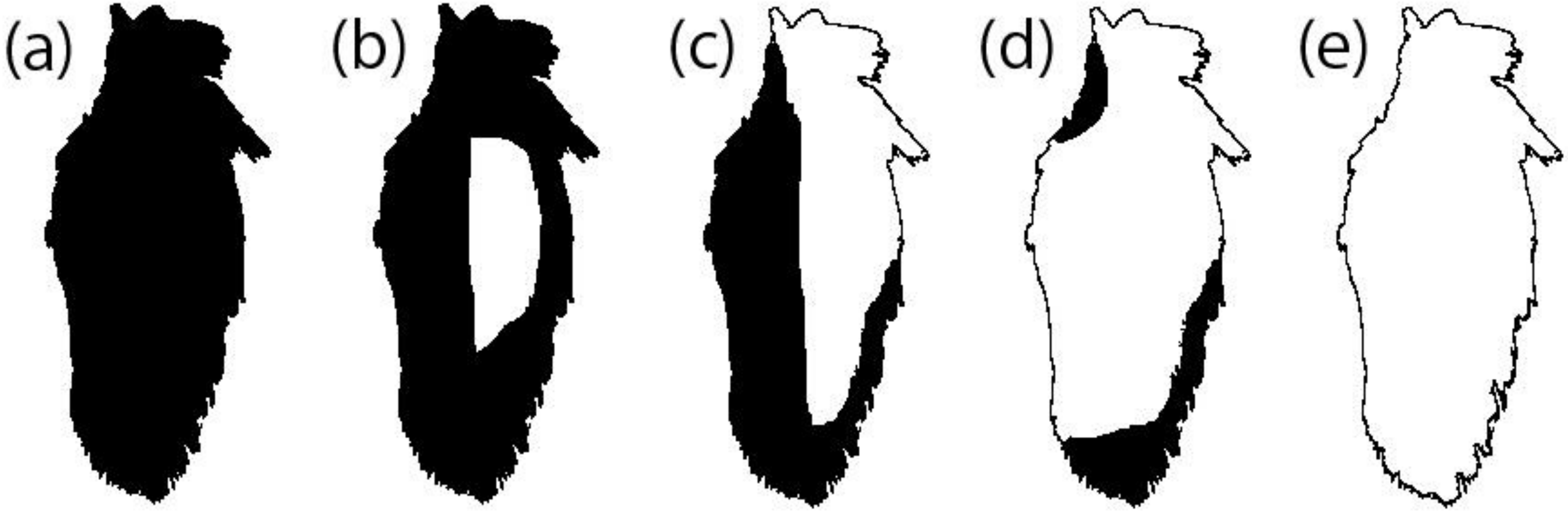


Fig. 2. Typical morphology of the wing patch on the greater coverts. These are scored (a)0, (b)1/4, (c)1/2, (d)3/4, (e)1.

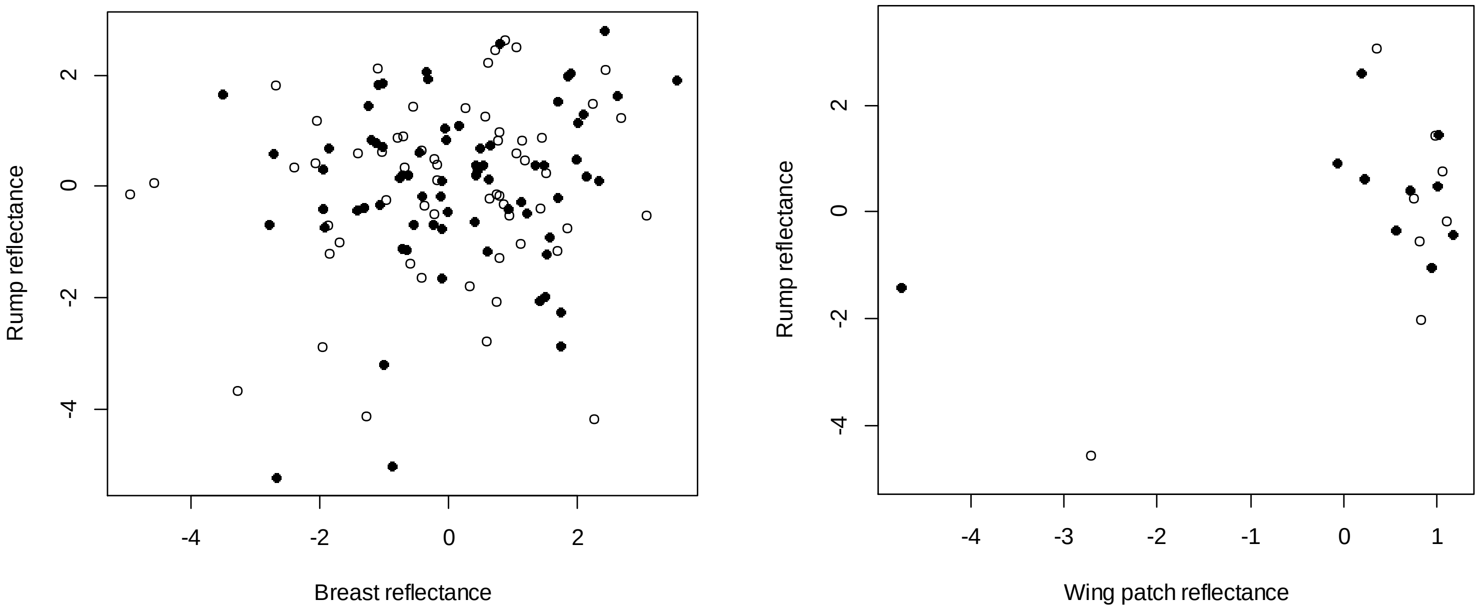


Fig. 3. Correlation between the breast reflectance component and rump reflectance component, and wing patch reflectance and rump reflectance. Black dots indicate mature males (second summer plumage or older), and white dots indicate yearlings.

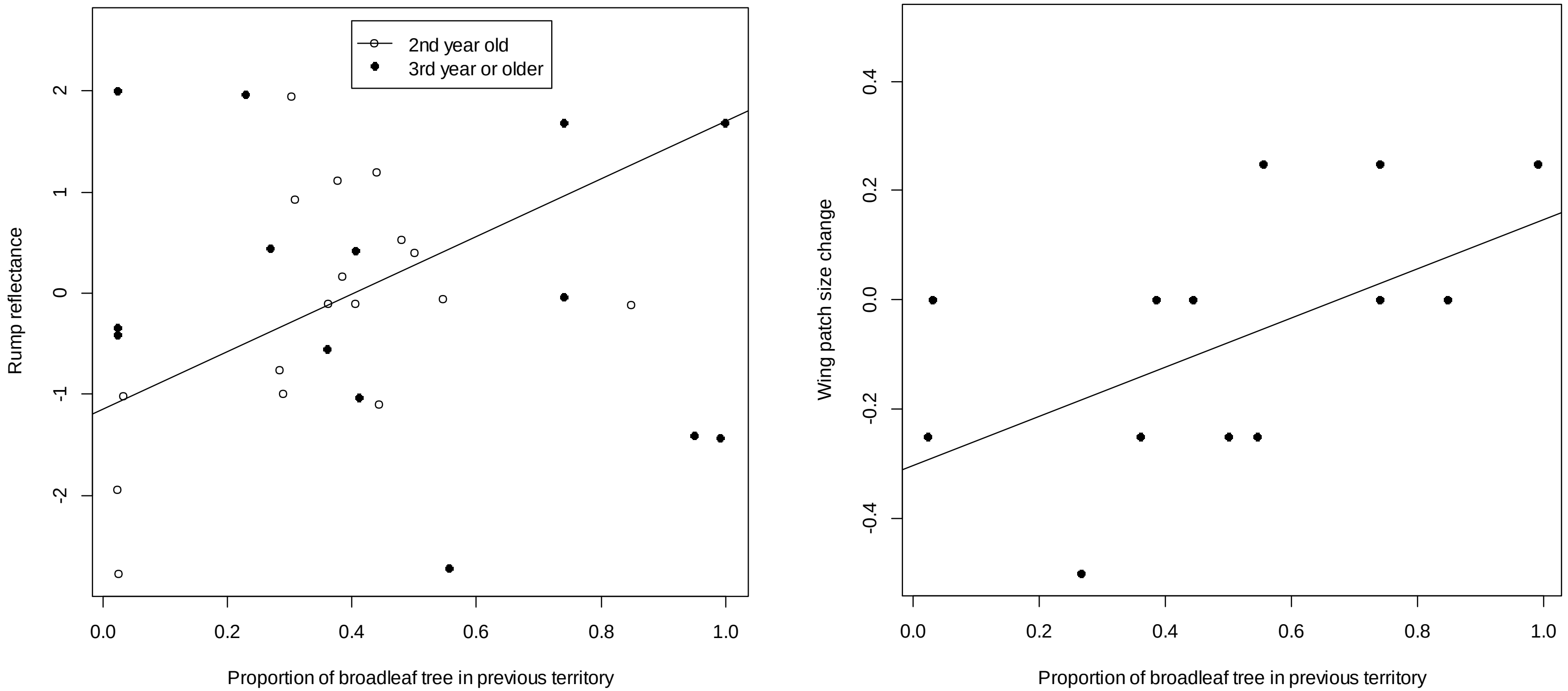


Fig. 4. (a) Correlation between the proportion of broadleaf trees in the territory in the past year and rump reflectance in the present year, and (b) between proportion of broadleaf trees in the territory in the previous year and wing patch size change.

Chapter IV

Delayed plumage maturation of the Narcissus Flycatcher *Ficedula narcissina*: signal status in conspecific male–male interaction

In most bird species, males are more conspicuous than females. Generally, it is assumed that elaborate male characteristics have evolved by sexual selection, because bright plumage plays an important role during male–male competition, because females prefer males with bright plumage (Darwin 1871, Lundberg & Alatalo 1992). As an exception to this general rule, the males of several passerine species breeds before getting the complete nuptial colouration on their plumage. This phenomenon is called delayed plumage maturation (DPM; Rohwer *et al*. 1980). There are two patterns of DPM: (1) a dynamic colour change because of physiological changes from dull (e.g. female-like plumage) to bright plumage and (2) gradational change in coloration (Hill 1996), where a young male has matured and immature feathers. Dynamic DPM in the body region (in macro view) is well studied (reviewed by Hawkins *et al*. 2012); however, the gradual DPM involving the retention of juvenile wing and tail feathers after partial moults is considered a non-interesting phenomenon (Hawkins *et al*. 2012). Thus, the functions of gradational DPM, comparatively, have not been well understood.

Several studies have hypothesized the adaptive function of DPM during the breeding season, such as female or juvenile mimicry and cryptic and status signals (Rohwer & Butcher 1988, reviewed by Hawkins *et al*. 2012). The status-signalling hypothesis (Lyon & Montgomerie 1986; reviewed by Senar 2006, Hawkins 2012) has been considered for explaining gradual DPM and sharp sexual dimorphism in yearlings. The hypothesis proposes that individuals signal their status to others through their colour. Dull males are able to avoid some costs from energy depletion, injury, and death by male–male interaction (Rohwer 1982, reviewed by Senar 2006). Bright males acquire some benefits from extra-pair copulations without aggressive male–male interaction (Lyon & Montgomerie 1986).

The Narcissus Flycatcher *Ficedula narcissina* is a small migrating passerine that breeds in Northeast Asia and winters in Southeast Asia (Töpfer 2006). The DPM of the bird varied among subspecies and populations (Kuroda 1925, Yamashina 1941), while colourations on the summer plumage of yearling Narcissus Flycatcher *F. n. narcissina* were distinct from mature males or females. The upper part of the body of a mature male is jet black. On the other hand, the primaries, secondaries, tertials, alula, coverts of yearling males had juvenile-like brown feathers, and the number of brown feathers that they had varied (Yamashina 1941, Okahisa *et al*. 2013). Our study aimed to confirm whether the gradual DPM of the Narcissus Flycatcher functions as a status signal in conspecific male–male interaction (intensity of aggressive behaviour and winning rate) by using 4 years' field observations.

Data were collected from 15 April to 15 June in 2010, 2011, 2012, and 2013 during the breeding seasons of the Narcissus Flycatcher in Fuji Primitive Forest, Central Japan (35°27′N, 138°38′E; 60 ha; 1140-m above sea level). The study area consisted of deciduous broadleaf forests (Japanese Oak *Quercus crispula*, Siebold's Beech *Fagus crenata*, and Japanese Blue Beech *F. japonica*) and evergreen coniferous forests (Japanese Cypress *Chamaecyparis obtusa* and Japanese Hemlock *Tsuga sieboldii*). Throughout the study period, I monitored singing males in the study area every morning (03:30–19:00). The day that a male was first recorded singing in a territory was assumed as the arrival day. In subsequent statistical analyses, I considered the early-arriving individual as the owner and late-arriving individual as the intruder. Two individuals arrived a same day and they fought. In this case, philopatric individual which occupied same territory in previous years was treated as the owner (n=4). Each male was lured into mist nets by song playback within two weeks from the arrival day. Males were ringed, for identification (ID) with a unique combination of colour-coded aluminium rings (authorized by the Ministry of the Environment Japan). The total number of brown feathers on each greater coverts, primaries, secondaries, tertials, and rectrices was used as an indicator of the brown area on individuals.

The method of dominance measurement and statistical analysis were based on the research of the Red-flanked Bush Robin *Tarsiger cyanurus* (Morimoto *et al*. 2006). I monitored 71 individuals in 4 years. One hundred aggressive behaviours between neighbouring territory owners were observed during the early period of each breeding season. The winner was considered as the dominant. After the fight, the winners were noted to first sing. The fight is considered lost when an individual escaped, signalling the end of fighting. The winner and loser were not determined when the intensity of aggressive behaviour gradually reduced and the fight ended indistinctly. Three categories were used to define the intensity of interaction: threatening, chasing, and fighting. A threatening interaction involved one male gazing at another male at a close range (0–3 m), making warning calls, and exhibiting bill clattering. When threatening escalated to high-intensity interactions, I recorded only the highest aggressive level of three categories.

All statistical tests were carried out using R v3.0.2. (R Development Core Team 2014). The effects of brown feather on the intensity of interactions and winning rate were tested by likelihood ratio chi-square test of generalized linear mixed models (GLMMs) with binomial errors and logit links. For testing the effect on the intensity, the types of interactions (fighting or chasing and threatening or others) were used as the response variables. For testing the effects on winning rate, win or lose was used as the response variable. When testing the effect on intensity, individual identity data (intruder ID and owner ID) were included in the model as random factors, to separate individual attributes other than plumage coloration (Morimoto *et al*. 2006). When testing the effects on winning rate, individual ID was used as the random factor. I tested the effect of variables by comparing the likelihood ratio of models, with and without the explanatory variables.

Fights with direct attack were observed less often when the intruder had more brown feathers (Fig. 1, GLMM, the number of brown feathers on intruder, $\chi^2_1 = 5.12$, $P = 0.02$); however, the number of brown feathers on the owners, age of the owners, and age of the intruder had no effect on the probability of direct attack (GLMM, the number of brown feathers on the owner, $\chi^2_1 = 0.76$, $P = 0.38$; the age of the intruder, $\chi^2_1 = 1.76$, $P = 0.19$; the age of the owner, $\chi^2_1 = 0.86$, $P = 0.35$). In addition, the direct attack was less likely to escalate into a fight when the intruder had more brown feathers (Fig. 1, GLMM, the number of brown feathers on the intruder, $\chi^2_1 = 6.53$, $P = 0.01$); however, the number of brown feathers on the owner, the age of the owner, and age of the intruder had no effect on the intensity of the direct attack (GLMM, the number of brown feathers on the owner, $\chi^2_1 = 0.40$, $P = 0.53$; age of intruder, $\chi^2_1 = 2.97$, $P = 0.08$; age of owner, $\chi^2_1 = 0.07$, $P = 0.79$).

The initially arriving owner was likely to win the fights (GLMM, $\chi^2_1 = 4.33$, $P = 0.04$). In addition, the effects of brown feathers on the winning rate differed between the owners and the intruders. The intruders having more brown feathers were at a disadvantage in the fights (Fig. 2, GLMM, $\chi^2_1 = 5.44$, $P = 0.02$). On the other hand, the brown feathers had no effect on the winning rate in the case of owners (Fig. 2, GLMM, $\chi^2_1 = 0.99$, $P = 0.32$).

The function of status signal is signalling their weakness to the competitor, and thus, avoiding strong interactions (Rohwer 1982, reviewed by Senar 2006). Our results suggest that the brown feathers on the yearling Narcissus Flycatcher function as a status signal in territory defence. This function is similar to that of status signals in other *Ficedula* flycatchers (i.e. brown and dark feather in the Pied Flycatcher *F. hypoleuca*, Järvi *et al*. 1987; and lack of red patch in the Red-breasted Flycatcher *F. parva*, Mitrus 2007). However, the presence of brown feather on Narcissus Flycatchers was significantly correlated with the intensity of fighting behaviour and the winning rate only when they were intruders, suggesting that the status signal is subjected to individual situations. Territorial ownership (prior residency effect and ownership advantage, Parker 1974, Kokko *et al*. 2006) strongly increased the winning rate of the Narcissus Flycatchers and probably motivated the territory defence. Mature males of most migrating birds arrived earlier than yearlings with DPM at the breeding site (Hill 1989). On the other hand, no significant trend in the arrival timing was observed between brown- and dark-feathered yearlings of the Narcissus Flycatchers (Okahisa *et al.* 2013). Thus, the status signal might be more important between age classes than among yearlings; however, the owner's age did not affect fighting behaviours. This might mean that the gradual DPM of the Narcissus Flycatchers evolved depending on the circumstance and the interaction between the ages is stronger than among yearlings, despite already functioning as a status signal within yearlings.

Hill (2002) and Hawkins *et al*. (2012) showed that it is important to consider the basic function of the plumage coloration in cases of DPM. The DPM of the Narcissus Flycatchers was observed as partial moulting in melanin-based pigmented area. Melanin-based plumage is predicted as the social status of an individual bird (reviewed by McGraw 2006). Further, it is correlated with the testosterone level; darker individuals showed a higher testosterone level (reviewed by McGraw

2006). Therefore, the correlation between the number of brown feathers and aggressiveness might be correlated with melanin pigmentation.

Thus, I conclude that the brown feathers on the Narcissus Flycatcher is a status signal, even though the moulting of migrating birds is influenced by natural selection pressure (energy cost of moulting, predations under migration), intersexual selection, and selection in the wintering area (Rohwer & Butcher 1988, Hill & McGraw 2006). The further exhaustive study is necessary to clarify the role of status signals.

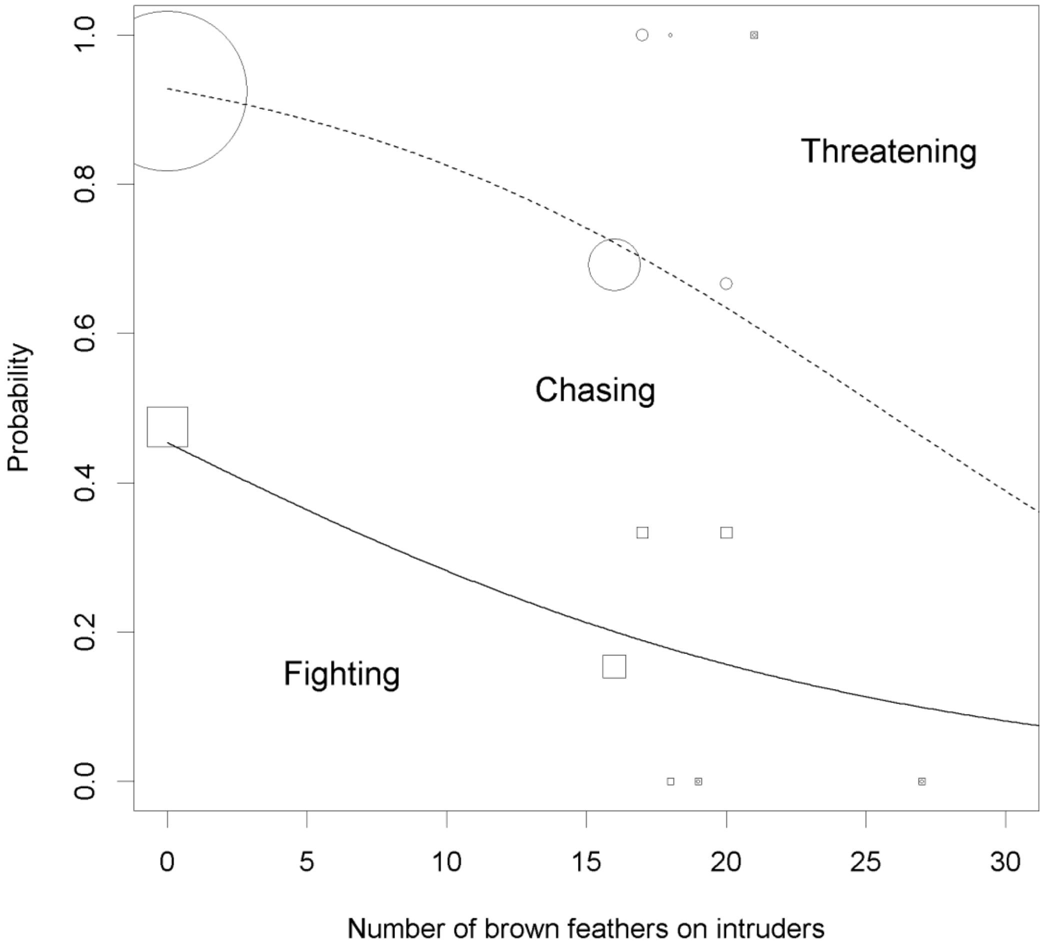


Figure 1. Probability of aggressive behaviour in relation to the number of brown feathers on the Narcissus Flycatchers. Circles indicate the probabilities of occurrence of chasing behaviour. Squares indicate the probabilities of occurrence of fighting behaviour. The sizes of the circles and squares represent the number of fights when calculating the probability. Solid line indicates predicted approximated curve of fighting behaviour by using generalized linear mixed models (GLMMs). Interrupted line indicates approximated curve of chasing behaviour by using GLMMs.

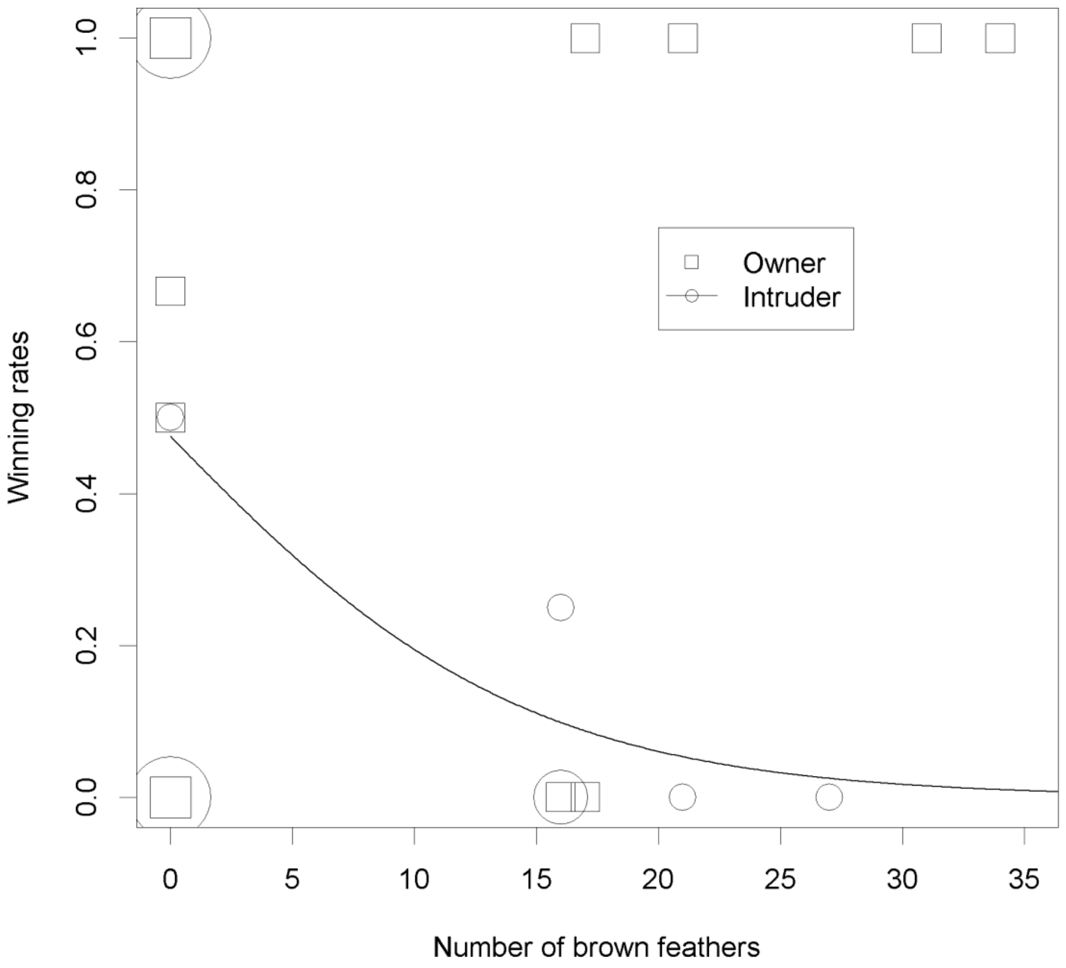


Figure 2. Winning rate in relation to the number of brown feathers on the Narcissus Flycatchers. Circles indicate the winning rate of the intruder. Squares indicate the winning rate of the owner. The sizes of the circles and squares represent the numbers of individuals at the same point. The line indicates predicted approximated curve of intruders by using generalized linear mixed models (GLMMs).

Chapter V

The multiple messages on mature and immature plumages of Narcissus Flycatcher *Ficedula narcissina* for the multiple receivers

In most bird species, males are more colourful than females. It is generally assumed that elaborate male characters have evolved by sexual selection, because brighter plumage is employed for male-male competition, or because females prefer males with brighter characters (Darwin 1871, Lundberg and Alatalo 1992, Hunt et al. 2009). For instance, when it comes to intra-sexual selection in migrating bird species, brighter males arrive earlier, get higher social status, and win in male-male competition (Hill 1989, Møller 1994, Reudink et al. 2009, Mitrus 2012). Thus they can occupy higher quality territory (Potti and Sagrario 1991, Pärt and Qvarnström 1997, Kokko 1999). For inter-sexual selection, bright plumage attracts females because it indicates material benefits for the female (better territory and parental care, Price et al. 1993, Pärt and Qvarnström 1997) or genetic benefits (as inheritance of the superior phenotype increases future offspring attractiveness and improved viability, Kokko and Lindström 1996, Török et al. 2003, Andersson and Simmons 2006).

The hypothesis that mate choice is based on several cues, instead of on single one, has received increased attention in recent years (reviewed by Candolin 2003, Hebets and Papaj 2005). Females may use different cues in different contexts (Jennions and Petrie 1997, Freeman-Gallant et al. 2010, Taff et al. 2013) and different male ornaments indicate different aspects of male quality (i.e. genetic, physical condition, feeding ability, and resource-holding power). In support of this, an increasing number of studies have found different ornaments to reflect different aspects of mate quality (multiple message hypothesis; Møller and Pomiankowsky 1993, Johnstone 1996, Török et al.

2003, Hegyi et al. 2010). For example, ornamental colours that are made up of different pigments often reflect different qualities; carotenoid pigments usually reflect physical condition (Hill and Montgomerie, 1994, Linville and Breitwisch, 1997, Olson and Owens, 1998, Navara and Hill 2003, McGraw 2006a), whereas melanin-based colours mostly reflect hormonal condition and social status (Jawor and Breitwish 2003, McGraw 2006b, but see also Guindre-Parker and Love 2013). Hence, they can signal different messages (reviewed by Candolin 2003). In addition to the multiple message hypothesis, Pryke et al. (2001) developed the idea that multiple messages can be a means of signalling multiple receivers. Considering intra- and inter-sexual selection, different plumage can act differently in relationships between males and males, or between males and females.

Yearling males of some bird species have dull, female-like plumage, but they often breed successfully (reviewed by Lyon and Montgomerie 1986, Hawkins et al. 2012). Such delayed plumage maturation (DPM) is assumed to have evolved so that yearling males can escape aggressive male competition (Hill 1989, Hawkins et al. 2012). When combined with the knowledge of multiple-trait signalling, multiple traits in birds with DPM may be signals to multiple receivers. (i.e., for attracting females and escaping from male competition). Moreover, even in inter-sexual selection, females show changes in emphasized traits for sexual selection depending on morphological traits related to DPM because some sexual traits of yearling males are not expressed but mature males have plumage with all of the sexual traits. This means that multiple-trait in male plumage may only not have individual functions, but combinations of the multiple traits may also have novel functions, or immature yearlings may have different signals to convey the same message as the plumage of mature males (backup signal, Møller and Pomiankowsky 1993, Johnstone 1996). Such interactions among multiple cues may be crucial to mate choice, but little study has been conducted on this subject (Candolin 2003, Hebets and Papaj 2005).

The Narcissus Flycatcher *Ficedula narcissina* is a small, sexually dimorphic migrating passerine species belonging to the genus *Ficedula*, which is one of the most studied bird group in terms of sexual selection and plumage function. It breeds in Northeast Asia and winter in Southeast Asia (del Hoyo et al. 2006, Töpfer 2006). It is socially monogamous, nest in wood cavities, and both parents care for nestlings and fledglings (Nakamura and Nakamura 1995, Okahisa *et al*. 2012). The male Narcissus Flycatcher has a bright yellow carotenoid-based area on the breast, and depigmented white patches on the wings. In addition, the summer plumage colour of yearling males and mature adults differs significantly. The entire upper part of the mature male wing feathers is jet black, but the primaries, secondaries, tertials, greater coverts, medium coverts, lesser coverts, and alula of yearling males have some female-like brown juvenile feathers, prior to their first spring moult (Kuroda 1925, Yamashina 1941), and the number of brown feathers which they have varies (Okahisa *et al*. 2013). Thus, the phenotypical variation of males is mainly dependent on carotenoid yellow, depigmented white, melanin black, and body size. Males display their breast plumage to attract females for pairing, raising their heads and shaking them slowly and smoothly. Males also flush their plumage colour in display flights to attract mates. In addition, males strongly attack their feathers in the male-male competition. Thus their plumages are probably important for intra- and intersexual selection.

The purpose of this study is to determine (1) the role of multiple traits with delayed plumage maturation signals for multiple receivers, (2) female focus on different male traits in yearlings and mature males when they mate. To achieve this, I examined the effect of phenotypic traits on arrival timing of males, effect of male traits on territory quality, and the effect of male traits on mating order, during four years of field research.

METHODS

Field research

Data were collected from 15 April to 15 August in 2010, 2011, 2012, and 2013 in the breeding season of the Narcissus Flycatcher, respectively, in Fuji Primitive Forest, Central Japan (35°27′N, 138°38′E; 60 ha; 1140 m above sea level). The study area consists of two forest types: deciduous broadleaf forest and evergreen coniferous forest. The deciduous broadleaf forests are dominated by old growth Japanese Oak *Quercus crispula*, Siebold's Beech *Fagus crenata*, and Japanese Blue Beech *F. japonica*. The evergreen coniferous forests are dominated by old growth Japanese Cypress *Chamaecyparis obtusa* and Japanese Hemlock *Tsuga sieboldii* (Okahisa et al. 2012). Arthropods (Diptera, Lepidoptera, Hymenoptera, Coleoptera) are more abundant in the broadleaf forest than the coniferous forest (Okahisa et al. in press), and the Narcissus Flycatcher in the broadleaf forest had larger clutch sizes than those in coniferous forest (Yuji Okahisa unpubl.).

I searched for singing males in the study area every morning (03:30–11:30) during the study. The day that a male was first recorded singing in a territory was assumed to be its arrival day (Mitrus 2007, Okahisa et al. 2012). In subsequent statistical analyses to examine the effect of moulting on arrival time, Julian dates beginning 20 April were used because the first flycatcher was observed on 20 April. I determined mating dates by observation of males and females making a contact call and moving together. Before mating, the display behaviour of male Narcissus Flycatchers was observed when the males were attempting to attract females.

Each male was lured into mist nets by song playback for up to two weeks from his arrival day within his territory. The age of each bird was determined by plumage characteristics (Okahisa et al.

2013). Males were uniquely ringed by a combination of aluminium (authorized by the Japan Environment Agency) and colour-coded rings. The following measurements were taken: body mass using a 30-g Pesola spring balance (to the nearest 0.1 g, Pesola AG), wing length (natural wing chord) and tarsus length with Mitsutoyo sliding digital callipers (o the nearest 0.1 mm, Mitsutoyo Corp.), and tail length with ruler (to the nearest 0.5 mm, Shinwa Rules Co., Ltd.). I recorded the moulting status (feather moulted in the wintering area or brown juvenile) of each greater covert, primary, secondary, tertiary, and rectrices on yearlings. The total number of brown feathers on these parts was used as an indicator of the moulting status of an individual.

I searched for singing males in the study area every morning (03:30–11:30) during the study periods. When I found the singing male, I followed it and plotted the singing location on maps. I located singing points by the colour marking on tree every 20 m made before spring migration of Narcissus Flycatcher and each of markings was located with GPS (accuracy was ± 8 m, eTrex Legend HCx, Garmin Ltd.). One observation trial was just 5 minutes and I repeated it every day. Finally, I calculated the minimum convex polygon of their song locations with ArcGIS 10.1 (ESRI) and considered this to be the flycatcher's territory. To estimate the territory quality of each male, the vegetation characteristics of the habitats were described in 50 randomly placed 10 m quadrats in each forest type (deciduous broadleaf and coniferous evergreen). The number of each tree species and their diameter at breast height values were recorded for each quadrat. Next, I calculated the area-weighted average rate of broadleaf trees of each territory with ArcGIS. It is known that this proportion for broadleaf forest is a suitable explanatory factor to predict prey abundance for insectivorous birds in our study area (Okahisa et al. in press).

Colour analysis

Upon capture, I plucked 5 breast feathers from males for spectrometric analyses. The feathers were placed on a black background for mimicking how they would naturally lay on the bird body (e.g. Keyser and Hill 1999). I obtained measurements of plumage colouration at the beginning of breeding. I measured reflectance between 300 and 700 nm using an Ocean Optics Jazz spectrometer (range 200–800 nm, Ocean Optics Inc.), illuminated with both UV (deuterium tungsten-halogen bulb) and visible (tungsten-halogen bulb) light sources, a WS-1 white standard (Ocean Optics Inc.). I used a bifurcated micron fibre optic probe at a 90° angle, and 1 mm from the feather’s surface. I used AVICOL software (Gomez 2006) for the analysis of reflectance. Initially, I summarized reflectance data (Fig. 1). I also used the model of Endler and Mielke for comparing the entire colour pattern of the bird (Endler and Mielke 2005, see also Peters et al. 2008). I calculated cone quantum catches based on spectral sensitivities of the four cones (VS: very short, S: short, M: medium, and L: long wavelength sensitive cones) used in colour vision (cone sensitivities for type U-eyes, Endler and Mielke 2005, Peters et al. 2008). I then divided each cone quantum catch by the sum of all four and transformed these according to Kelber et al. (Kelber et al. 2003), to summarize three independent relative cone catches (x, y, and z, Peters et al. 2008). Higher values of x represent greater stimulation of the L cone and lower stimulation of the M cone; higher y values represent greater stimulation of the S cone; and higher values of z greater stimulation of the VS cone (Endler and Mielke 2005, Peters et al. 2008). These relative cone catches can be represented as points in the tetrahedral avian visual space (Peters et al. 2008). I calculated the first principal component (PCxyz, see Peters et al. 2008), that explained 81% of the variation (Table 1). I used the principal component of breast plumage as an indicator of breast plumage color for analysis.

I also determined the white patch on the wing by scoring the size on each feather from the greater coverts and tertials (Fig. 2), because the greater coverts and tertials overlap each other, and move easily, thus calculating the real total area is difficult. I used the sum of each wing patch size as an indicator of whole white patch size.

Statistical analysis

All statistical tests were carried out using R ver. 3.0.2. (R development core team). This was done to test the morphological repeatability of breast plumage colour with Pearson's correlation test and compare the morphological traits to the previous and present year. I also tested the repeatability of white patch size with a Kendall tau rank correlation coefficient and compared the morphological trait to the previous and present year. I used lme4 package lmer to fit general linear mixed models (LMMs) with Gaussian error and the identity link function (Bates et al. 2014) for comparing morphology between mature birds and yearlings. In this case I used male age group as explanatory variables and study year and IDs of individuals were used as random factors. P-values for each factor were obtained from a likelihood ratio F-test of full models.

To examine the effect of male morphology on their arrival, territory quality, and mating order, I used lmer to fit general linear mixed models (LMMs) with Gaussian error and the identity link function. In this case, I used package lmerTest in R (Kuznetsova et al. 2013) for calculating the Satterthwaite's approximation to degrees of freedom. I used the number of non-moulted brown feathers, PC score of breast plumage colour, white patch size, tarsus length, and wing length as explanatory variables. Study year and IDs of individuals were used as random factors. Because of the high correlation between wing length and tail length ($r = 0.55$, $t = 7.40$, DF = 128, $p < 0.001$), I excluded tail length from this analysis.

RESULTS

Yearling males had significantly shorter wing chord, shorter tail length, and lighter body mass than those of mature males (Table 2). In addition, the white patch size on mature males tended to be larger than those on yearlings. The breast plumage colour and tarsus length were not different between the ages respectively. Since the change in the breast plumage among years was marked, there was no correlation in plumage colours between breeding seasons ($r = -0.19$, $t = -0.71$, DF = 14, $p = 0.49$). However the change in white patch size between years is small and the white patch score was dependent on individuals (tau = 0.74, $z = 3.70$, DF = 15, $p < 0.001$). There were no correlation between the breast plumage and white patch size of mature individuals (tau = -0.10, $z = -0.95$, DF = 58, $p = 0.34$) and yearlings (tau = 0.02, $z = 0.17$, DF = 49, $p = 0.86$). There was no correlation between breast plumage colour and number of non-moulting brown feathers (tau = 0.02, $z = 0.24$, DF = 49, $p = 0.80$), but the number of brown feathers was negatively correlated with white patch size (tau = -0.29, $z = -2.64$, DF = 49, $p = 0.008$).

The mature males arrived at the site earlier than yearlings (LMM: $F_{1, 203} = 50.83$, $p < 0.001$). The yearling males having larger body mass arrived at the breeding site earlier (Fig. 3, Table 3). The other morphological traits were not correlated with the arrival timing of yearlings (Table 3). There were no relationships between morphological traits and the arrival date of mature males (Table 3).

The yearlings that had moulted more feathers occupied territories with higher proportions of broadleaf trees (Table 3, Fig. 4), while other traits did not affect territory. On the other hand, there was no relationship between the proportion of broadleaf trees and the traits of mature males (Table 3). There was no significant difference between the proportion of broadleaf trees in the territories of mature males and yearlings (LMM: $F_{1,174} = 0.15$, $p = 0.70$).

On average, the mature males mated earlier than yearlings (LMM: $F_{1, 97} = 9.98$, $p = 0.002$). The effect of male traits on mating order was different between mature males and yearlings. Yearling males occupying higher proportion of broadleaf trees and having brighter breast plumage mated earlier (Table 3, Fig. 5), but other traits did not affect mating order (Table 3). In contrast, mature males having larger white patches on their wings mated earlier, but other traits did not affect mating order in the mature male populations (Table 2, Fig. 5).

DISCUSSION

The multiple plumage traits of the Narcissus Flycatcher had different functions, territory occupancy between males and female mate choice. A correlation between male phenotypic traits and territory characteristics (prey abundance, nest sites, or other resources) has been found in several species. Candolin (2003) argued that male and territory (resource) traits often back each other up as signals of male quality (e.g. Hill 1988, Pärt and Qvarnström 1997, Wolfenbarger 1999). However, the opposite result is equally common (e.g. Alatalo et al. 1986, Reid and Weatherhead 1990, Buchanan and Catchpole 1997), which indicates that a correlation between the traits is not a general trend (Candolin 2003). In this study, I only found a correlation between male phenotypic traits and territory characteristics in yearling males, but there was no such correlation in mature males. The Narcissus Flycatcher has strong territory fidelity and mature males return to the same territory (Yuji Okahisa *unpbl*). In contrast, yearlings must choose their territory for the first time, thus the intra-sexual competition among yearlings might be stronger.

There is a trade-off between sexual trait expression and body condition for yearlings of the Narcissus Flycatcher. Moulting in the wintering area causes a negative effect on body condition (Okahisa et al. 2013). Less moulted individual were in better condition. The better condition made them able to arrive at breeding sites earlier, although I was unable to find any effect of arrival timing on their territory quality. Conversely, individuals that moulted more in the wintering grounds were in worse condition, and this worsened condition caused their later arrival. The individuals that moulted to a greater extent in the wintering grounds occupied better territory in our study site. This is probably because melanin-based colour mostly reflects social status and resource-holding power (Fitze and Richner 2002, Jawor and Breitwisch 2003, Hawkins et al. 2012). While, Forstmeier (2002) described Dusky Warblers *Phylloscopus fuscatus* with less resource-holding power arrived at breeding sites earlier to secure prior ownership and thus compensate for the difference in resource-holding power. Considering such a trade-off via resource-holding power and arrival timing (Forstmeier 2002, Candolin and Voigt 2003), it would be better for females to focus on the territory than to focus on the variety of delayed plumage maturation. Because estimating the resource holding power with delayed plumage maturation could cause selection error caused by prior ownership.

The carotenoid-based colours of male Narcissus Flycatchers changed annually and there was no significant difference between mature birds and yearlings. This might indicate that it is difficult even for mature males to obtain sufficient carotenoids from prey. Moreover, the colour could convey the condition of mature and yearling males; however, the throat colour did not influence the mating order of mature males, although females focused on the carotenoid-yellow plumage when mating with yearlings. Carotenoid-based colours are recognized as having an important signalling function in bird ecology. Animals can only obtain the carotenoid from their diet (Goodwin 1984). The amount deposited in ornaments may thereby reflect the individual's ability to acquire and assimilate these pigments (Peters et al. 2008). Carotenoid-based colour signals parental ability, foraging ability, and health (Hadfield and Owens 2006, reviewed McGraw 2006a). In summary, focusing on carotenoid-yellow plumage and territory quality when they choose partners might influence the decision making of females seeking to increase clutch size and parental care of nestlings (Direct benefit, Price et al. 1993, Andersson and Simmons 2006).

In contrast, females focussed on white patch size of mature males with purely black upper parts. The white patch size of the Narcissus Flycatcher showed considerable variation among individuals; the patch was slightly larger in elder male groups, similar to other *Ficedula* flycatchers (Potti 1993, Török 2003, Laczi et al. 2011). The depigmented white patch of the *Ficedula* flycatcher can weakly reflect the prior condition of individuals (Török 2003), but is usually treated as a sexual trait indicating genetic quality, with a larger white patch influencing extra-pair paternity and mating success (Potti 1993, Sheldon et al., 1997, Sheldon and Ellegren 1999, Sanz 2001, Sirkiä and Laaksonen 2009, de Heij et al. 2011). Thus, choosing the individuals with larger white patches might not be selecting for better-conditioned males, but for increased genetic benefits such as inheritance of the phenotype for future attractiveness and improved viability (de Heij et al. 2011, Laczi et al. 2011). The tendency of female preference for larger white patches could be correlated with female preference for elder individuals. Kokko and Lindström (1996) predicted using a mathematical simulation that the female mate preferences for elder males evolved by female preference for the genetic quality of viability. This knowledge suggests that even if the female preference for larger white patches is correlated with male age and other traits related to delayed plumage maturation, the effect of the male white patch on paring order is caused by female preference for genetically superior individuals.

There might be reasons why females used different cues for the male of different age groups. First, depigmented white patches are expressed after the post-breeding moulting of some yearlings (Okahisa et al. 2013), thus females are not able to assess the genetically determined patch size of yearlings in some cases, and focussing on the white patch of yearlings may be costly and misleading for females. Therefore, it might be unreliable for females to choose yearling mates with white patches. Second, the tendency of females to select for direct benefits when they mate with yearling might be caused by female decision making, including the possibility of extra-pair paternity. It is widely known that females prefer males that provide better parental care and better territory, but they choose genetically superior males for extra-pair copulation (Weatherhead and Boag 1995, reviewed by Westneat et al. 1990, Petrie and Kempenaers 1998, Griffith et al. 2002, Westneat and Stewart 2003). I was not able to determine the effect of extra-pair copulation on the mating pattern of these results, but females might compensate genetic benefit by extra-pair copulation when they chose yearling male with material benefit. Yearling males might be more cuckolded, as they are in other *Ficedula* flycatchers (i.e. Moreno et al. 2010, but see also Rätti et al. 1995). Lastly, It is argued that the association between condition and carotenoid-ornamentation might decline with age because the carotenoid saturation with age masked the effect of male condition on ornamentation (Grunst et al. 2014, see also Badyaev and Duckworth 2003), and it could make signals “dishonest” for female (Copeland and Fedorka 2012). Our results apparently support this argument, but the variance of the carotenoid ornamentation was not different between yearlings and mature males in the Narcissus Flycatcher. In addition, the carotenoid saturation with age was not found. Thus, the difference in ornamentation function in different male age groups could not be associated with differences in the reliability of carotenoid pigmentation.

In this study, a correlation between the phenotypical traits was not found in mature males. Even though the moulting status was correlated with the white patch size of yearlings, the messages of the depigmented white patch, melanin black and yellow breast were different as has been explained above. Thus, our results support the multiple message hypothesis (different signals convey information on different properties of male quality; Møller and Pomiankowski 1993, Johnstone 1996, Candolin 2003). Moreover, the result that different male traits act in female choice on male age groups suggests that there are hierarchical interactions (sequential interaction, Candolin 2003) between DPM and sexually selected traits. In this case, females might firstly check for the presence of brown feathers of a male, then focussed on breast yellow or depigmented white patch. A hierarchical use of cues in mate choice have been hitherto suggested in Barn Swallow *Hirundo rustica*; the female pay strong attention on male song when the male has longer tail (Møller et al. 1998). Our finding also suggests that the DPM may act to discern the context for receivers.

The number of moulted feathers, a trait of delayed plumage maturation, functioned in other elements of male competition such as arrival timing and territory occupancy. On the other hand, the yellow plumage and white patches attracted females. These results support the hypothesis that multiple signalling can be lead to consistency among signalling multiple receivers (Pryke et al. 2001, Andersson et al. 2002, Guindre-Parker et al. 2013); in this case, the different traits functioned in different relationships between males and females. A function of delayed plumage maturation is escape from strong male-male competition (status signaling: e.g. Hill 1989, Morimoto et al. 2006, reviewed by Hawkins et al. 2012), thus the multiple receiver hypothesis might be generally accepted in bird species having delayed plumage maturation. Additional empirical study is required to confirm this.

Our results indicate (1) that the multiple traits of male plumage convey different aspects of male quality and females receive the multiple messages hierarchically, and (2) that the different male traits function in different relationships. These results indicate the strong context dependency of sexual ornamentation in the Narcissus Flycatcher. Although I identified links among male morphological traits, ecological traits, and female choice; behavioural and experimental study will be needed to reveal the detailed functions and evolution of plumage colour in *Ficedula* flycatchers in the future.

Table 1. Results of the principal component analysis of breast plumage colour

	Comp.1	Comp.2	Comp.3
x	0.98	0.08	0.18
y	0.89	0.43	-0.13
z	-0.82	0.56	0.07
Standard deviation	1.56	0.71	0.23
Proportion of variance	0.81	0.17	0.02
Cumulative proportion	0.81	0.98	1.00

Table 2. Morphological differences between mature and yearling males (mean±SD). F and p calculated likelihood test of generalized linear mixed model.

Character	Yearling		Mature				
	Mean (±SD)	n	Mean (±SD)	n	F	DF	p
White patch size score	2.90±0.7	51	3.12±0.5	61	3.9	1, 110	0.05
Breast plumage colour	-0.01±1.5	51	-0.02±1.7	61	0.0	1, 110	0.84
Number of brown feathers	19.89±5.5	59	0.0±0.0	71	1152.6	1, 128	<0.001
Wing chord (mm)	74.59±1.4	59	76.40±1.8	71	42.3	1, 128	<0.001
Tail length (mm)	51.01±1.5	59	51.44±1.7	71	4.0	1, 128	0.05
Tarsus length (mm)	16.29±0.5	59	16.37±0.4	71	1.1	1, 128	0.29
Body mass (g)	13.91±0.7	59	14.29±0.9	71	4.4	1, 128	0.04

Table 3. Results of the generalized mixed model analysis on arrival date, territory quality, and mating order. Bold characteristics indicate the factors are significant ($P<0.05$).

	Arrival date				Territory				Mating order			
	Yearling n = 42		Matured n = 53		Yearling n = 35		Matured n = 45		Yearling n = 27		Matured n = 32	
	F	p	F	p	F	p	F	p	F	p	F	p
Breast plumage color	0.00	0.94	2.21	0.14	0.06	0.80	1.50	0.23	**5.98**	**0.03**	1.29	0.27
White patch size	0.83	0.37	0.13	0.73	0.00	0.97	0.16	0.70	0.00	0.95	**4.75**	**0.04**
Number of brown feather	0.10	0.75			**6.63**	**0.02**			0.08	0.78		
Body mass	**4.35**	**0.05**	0.92	0.34	0.02	0.89	0.17	0.69	0.46	0.51	1.33	0.27
Wing chord	0.00	0.97	0.44	0.51	2.08	0.16	2.99	0.10	0.05	0.82	0.11	0.74
Tarsus length	0.00	0.99	0.78	0.38	0.32	0.57	0.72	0.40	1.53	0.23	0.00	0.94
Arrival date					0.03	0.87	0.20	0.66	2.37	0.14	1.02	0.32
Proportion of broadleaf tree									**4.61**	**0.05**	1.74	0.20

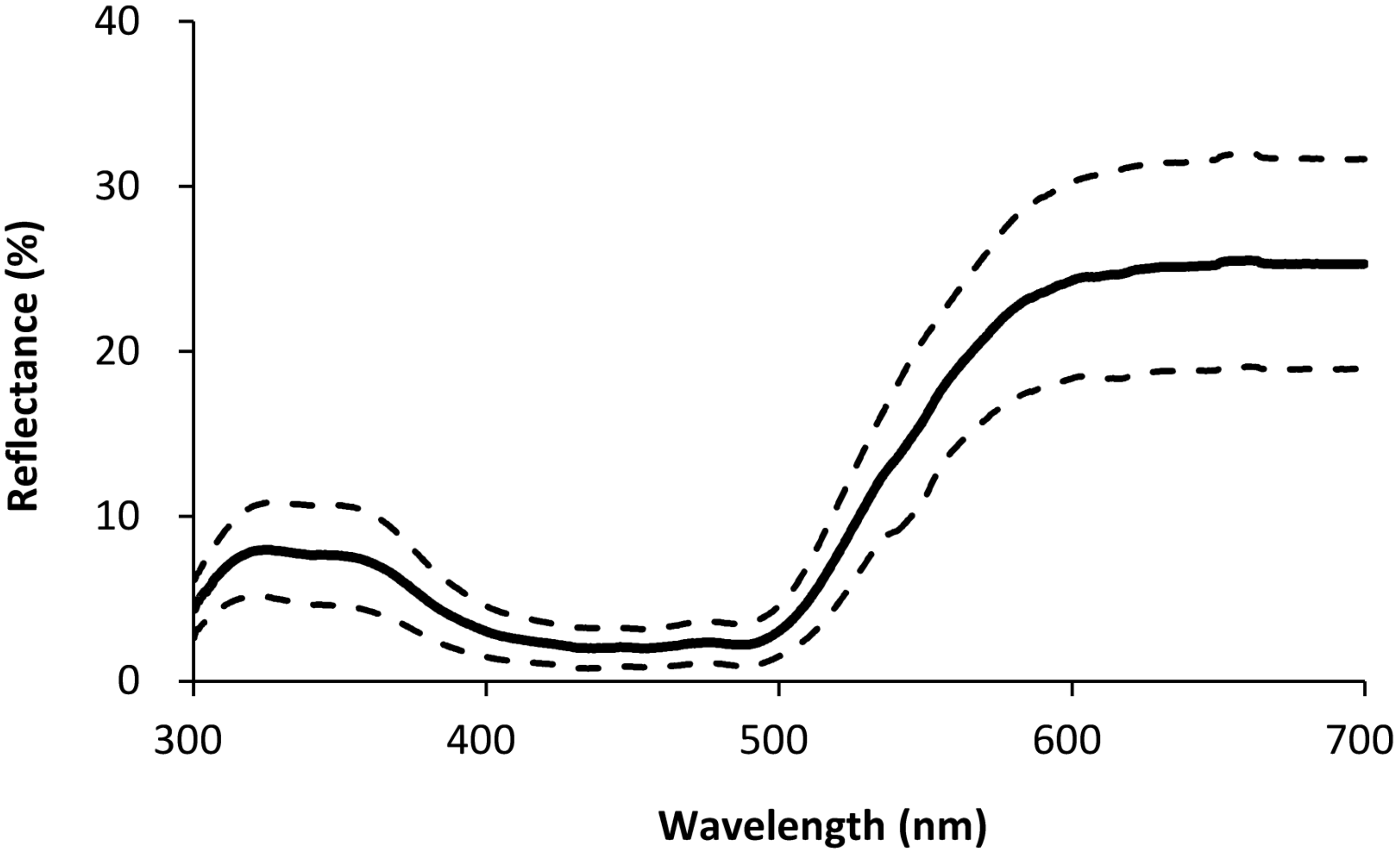


Figure 1. Reflectance spectra of the reddish-yellow breast patch of the Narcissus Flycatcher *Ficedula narcissina*. The solid line indicates average wavelength; dotted lines indicate SD.

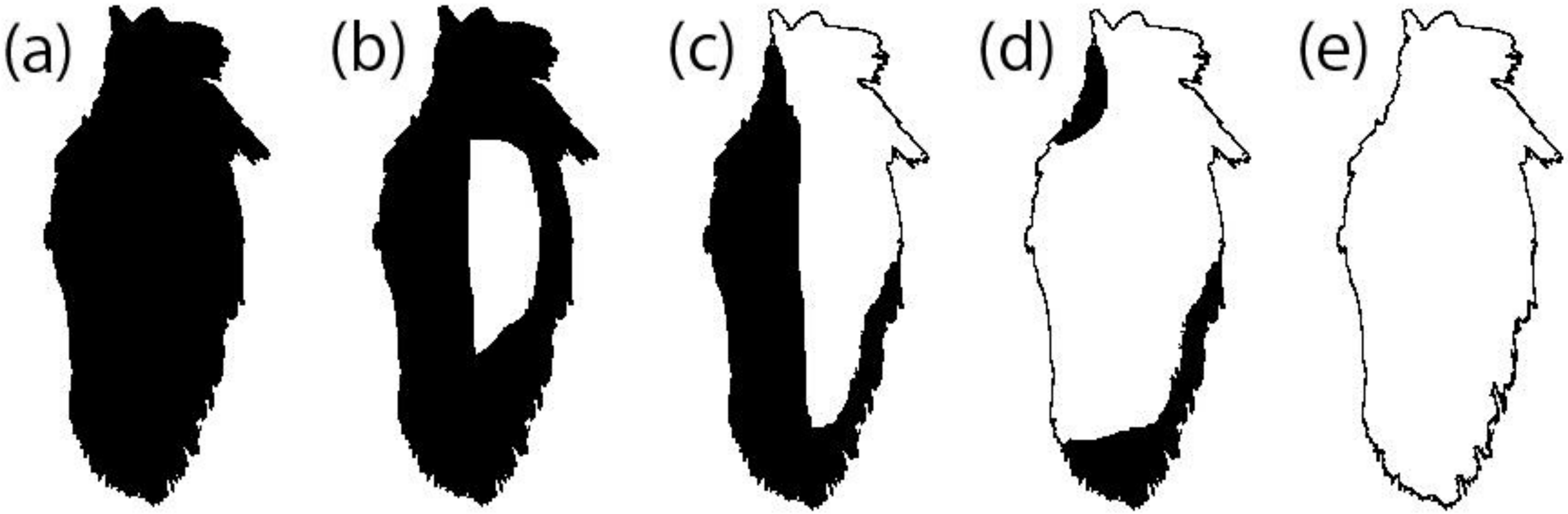


Figure 2. Typical morphology of the white patch on the greater coverts. These are scored (a)0, (b)1/4, (c)1/2, (d)3/4, and (e)1.

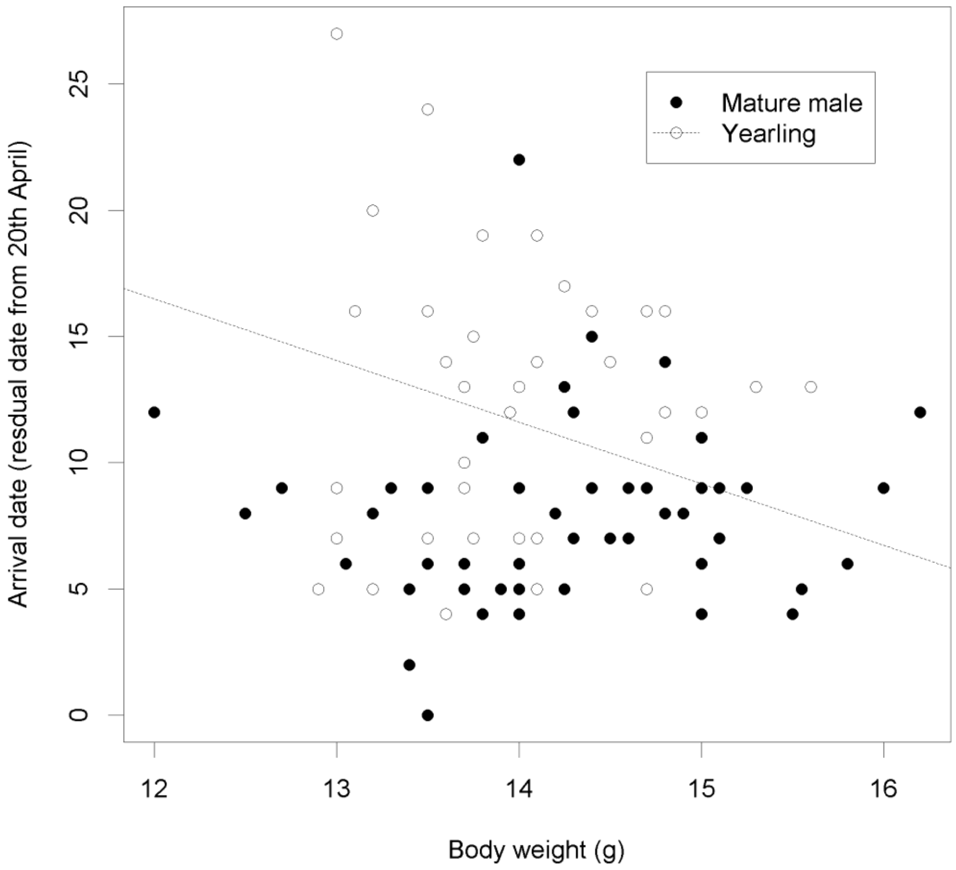


Figure 3. Body mass and arrival date of Narcissus Flycatchers. Dots indicate mature male, circles indicate yearling males. Dash line means regression line of yearlings.

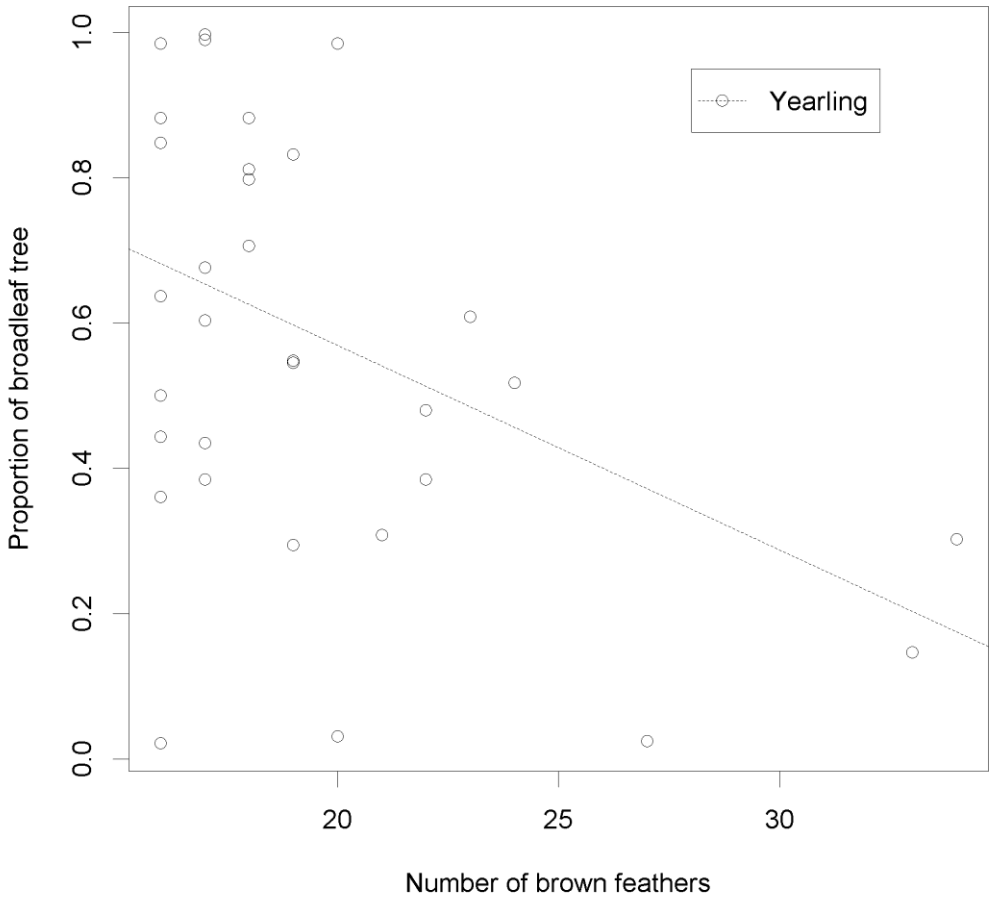


Figure 4. Proportion of broadleaf tree in each territory and number of brown feathers on yearling males' body. Dash line means regression line of yearlings.

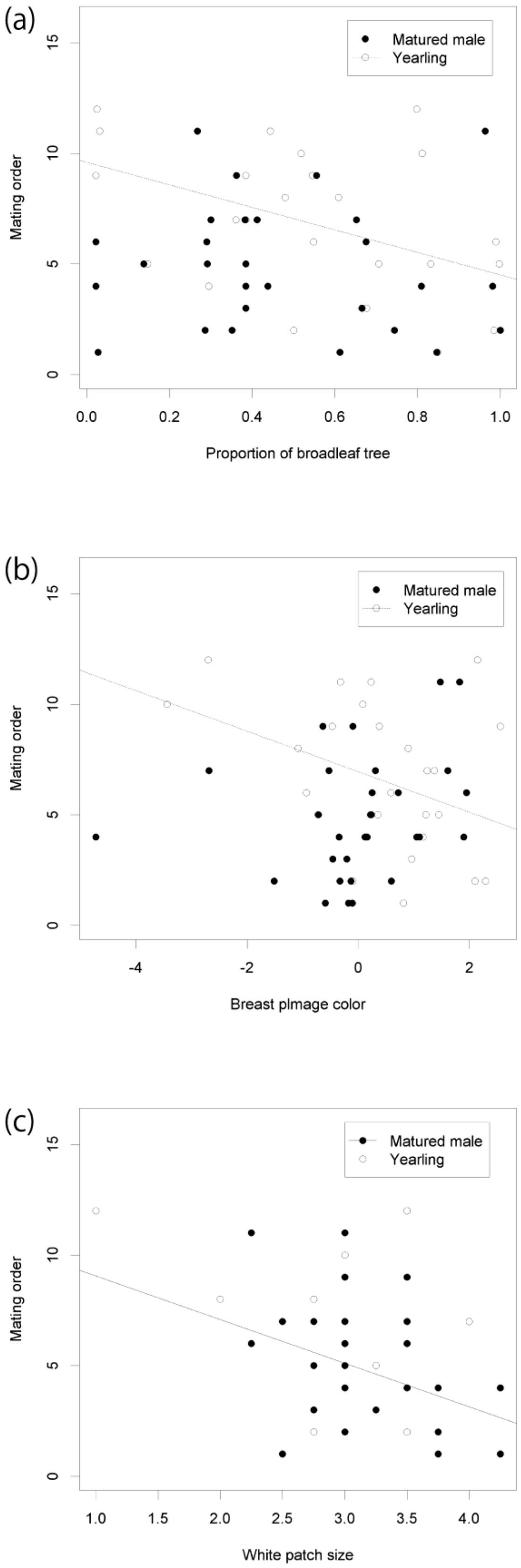


Figure 5. Mating order and male traits (a) proportion of broadleaf trees, (b) breast plumage, and (c) white patch size). Dots indicate mature male, and circles indicate yearling males. Solid line indicates regression line of mature male. Dash lines indicate regression line of yearlings.

Chapter VI

Reproductive strategy of mature and yearling male: the nest predation experience enhance the benefit of territory fidelity of Narcissus Flycatchers *Ficedula narcissina*

Animals return to, and tend to stay in familiar habitats (Greenwood 1980). Such area-restricted site fidelity has fundamental consequences for many ecological processes and evolutionary biology (Börger et al. 2008). The site fidelity or dispersal is important in gene flow and population dynamics (dynamic demography, reducing the likelihood of interaction with kin, bet hedging, and escaping local unfavourable conditions, reviewed by Matthysen 2012). In addition, the decision of the stay or dispersal influences individual habitat selection, fecundity, and survival rate (Hoover 2003). Thus, ecologists have been attracted to exploring site fidelity, which is of perennial interest (Greenwood and Harvey 1982).

In the instance of breeding dispersal of territorial bird species, even though migratory birds have high dispersion ability, they tend to return to breeding areas where they bred in prior years (site fidelity, Houston 1974), and sometimes males return to a specific breeding territory (territory fidelity, Hoover 2003). Generally, this phenomenon is determined by the cost and benefit of dispersal. The most widely accepted explanation is that site fidelity is directly beneficial, since acquired skills in finding a good site, and occupying territory in a familiar area improves reproductive success with experience. There is also general agreement that site fidelity is advantageous in individual dispersal, because the traveling cost of energy, predation risks, and higher competition increase during the search for a new breeding site (Pärt, 1991; Oro et al.

2011; Matthysen 2012). However, the cost and risk of abandoning a familiar area on relinquishing information, and a lack of information on immigration to an unfamiliar area, is not yet adequately understood.

Nest predation is the main reason of reproductive failure in most bird species (Ricklefs 1969; Pöysä et al. 2001), and avoidance of nest predation is the most important factor in the decision-making of avian breeding dispersal (Jackson and Rohwer 1989; Powell and Frasch 1999). If there were neither predation at the breeding site, or nest failure, philopatry would be beneficial for birds. However, when individuals face nest predation, they choose from two options: (1) moving to a new territory (win-stay/lose-switch strategy, Switzer 1993), or (2) remaining in the same territory (always stay strategy, Switzer 1993). If emigrants can find a high-quality site and drastically increase reproductive success, the dispersal is adoptive than philopatric (the “cost of philopatry” hypothesis, Morris 1992). However, if philopatric birds can highly improve their skills to avoid nest predation, the philopatry is advantageous in individual dispersals (“resident fitness” hypothesis, Anderson 1989). Thus, the ability to select nest sites with reduced predation risk should be the most important factor in individual breeding dispersal and reproduction.

High return rate and site fidelity of migrating birds is well known (Greenwood and Harvey 1982). It suggest not only the experience of breeding, but also the local distinctive experience (e.g., accuracy for nest site selection, knowledge of predator) is important to improve reproductive success. Philopatric individuals experience breeding in defined areas. When reproduction is successful, birds are likely to return to the same territory, because of the ease in avoiding nest predation; even when nests are depredated, birds can get some information about nest predation. Therefore, philopatric birds would select a suitable nest site to avoid nest predation during the next breeding season by using knowledge of local predators actually present in an area. On the other hand, immigrants can suffer from a lack of information at an unfamiliar site, for example, nesting in an unsuitable location. Moreover, if emigrants immigrate to an area where the predation risk and trends are different from their previous breeding site, their breeding experience can cause unsuitable nest site selection.

To understand the effect of dispersal without any local experience, I compared the nest site selection and reproductive success of philopatric matured males, matured immigrant males, and yearlings, and studied improvements in suitable nest site selection in philopatric individuals of the Narcissus Flycatcher *Ficedula narcissina* during 5 years of field research. At first, I determined the nest predation trends, and then compared the nest site selection, predation rate, and reproductive success of philopatric matured males, matured immigrant males, and yearling Narcissus Flycatchers.

METHODS

Data were collected from 15 April to 15 August in 2008, 2009, 2010, 2011, and 2012 in the breeding season of the Narcissus Flycatcher in the Fuji Primitive Forest, central Japan (35° 27′ N, 138° 38′ E; 60 ha; 1140 m above sea level). The forest in the study area consists of two types: a deciduous broadleaf forest and an evergreen coniferous forest. Deciduous broad-leaved forests are dominated by old-growth Japanese Oak *Quercus crispula*, Siebold’s Beech *Fagus crenata*, and Japanese Blue Beech *Fagus japonica*. The evergreen coniferous forests are dominated by old-growth Japanese Cypress *Chamaecyparis obtusa* and Japanese Hemlock *Tsuga sieboldii* (see Okahisa et al. 2012, 2014 for detail). Arthropods (Diptera, Lepidoptera, Hymenoptera, and Coleoptera) are more abundant in broadleaf forests than coniferous forests (Okahisa et al. 2014).

Each male was lured into a mist net using song playback. The age of each bird was determined by plumage characteristics (Okahisa et al. 2013). Males were uniquely ringed using a combination of aluminium (authorised by the Ministry of the Environment Japan) and colour-coded rings. Every year, approximately 50 territorial males were captured for study. The status of philopatry was determined by the colour bands. When ringed individuals returned to the same territory the next year, they were treated as philopatric. In this case, the difference of territory gravity was 35.12 ± 19.96 m. Ringed individuals were never observed to change territory location between the years at the study site nor did the ringed individuals occupy a territory that different individuals had occupied in a prior year. On the other hand, non-banded individuals immigrate and occupy where ringed individuals have occupied in prior year, and these were classified as immigrants. The incidence of non-ringed individuals occupying where non-ringed individuals occupied in a prior year could not be determined, and thus their data was excluded in analysis of philopatry. The age of individuals was determined by plumage characteristics, and distinguished between immigrants and yearlings (Okahisa et al. 2013).

Singing males were sought after in the study area every morning (03:30–11:30) during the study periods. When singing males were found, they were followed, and their singing location plotted on a map. Singing points were located by using the colour marking on trees every 20 m, made before spring migration of the Narcissus Flycatcher, and each of the markings were located with GPS (Garmin, eTrex legend, accuracy was ±8 m). I followed singing male only 5 min, and was repeated every day. Finally, the minimum convex polygon of their song locations was calculated with ArcGIS 10.1 (Environmental Systems Research Institute) and considered as being the flycatcher's territory. To estimate the territory quality of each individual, the vegetation characteristics of Narcissus Flycatcher habitats were described in 50 randomly placed 10 m quadrats in each forest type (deciduous broadleaf and coniferous evergreen). The number of each tree species and their diameter at breast height (DBH) values were recorded for each quadrat. Next, the area weighted average proportion of broadleaf trees of each territory was calculated with ArcGIS. It is known that the proportion of broadleaf forests is a suitable explanatory factor to predict prey abundance for insectivorous birds in the study area (Kanae Okubo, unpublished).

Nests were located by following adults exhibiting nest-building behaviour (more detail in Okahisa et al. 2012). Upon finding a nest, the following data were collected: (1) nest site type (half cavity, full cavity, chimney, or shelf; Okahisa et al. 2012), (2) height of nest entrance above ground (as measured by laser rangefinder; Laser 550AS, Nikon), (3) condition of the tree fragment with the cavity (live or dead), (4) DBH (as measured by tape), (5) forest type of nest site location (deciduous broadleaf forest or coniferous evergreen forest), and (6) reproductive success (nest predation, clutch size, number of chicks, and fledglings). I monitored nests every 2–3 days. To monitor nests in high positions in trees, a digital camera on a long pole was used. The clutch size could not be determined if the nest was depredated before the female began incubation or the nest was found during the nestling stage. On the contrary, only when the nest was depredated before egg hatching could the clutch size be recorded. Only 3 nest sites were used twice and were included in the analysis. To calculate the mean clutch size and brood size, the data for nest failure (0 eggs and 0 nestlings) was excluded. The average number of fledglings was calculated using brood size and the probability of a successful nest. The identification of fledglings was also recorded. Reproduction was considered successful when fledglings fed by parents were observed.

All statistical tests were carried out using R version 3.0.0 (R development core team 2013). To determine the trend of nest predation (depredated or successful), the likelihood ratio chi-squared test of generalised linear mixed models (GLMMs) with binomial error and logit link function was used. The nest site type, height of nest entrance above ground, condition of the tree fragment with the cavity, DBH of tree, forest type of nest site location, and study year were used as explanatory variables. The individual's ID was considered to be a random factor. The chi-squared test was carried out by comparing the deviance of the full model and the model without this factor. To test the effect of nest predation experience on the return rate of males, a likelihood ratio chi-squared test of GLMMs (binomial error, logit link function, and study year as a random factor) was used. In this case, the model that included the previous reproduction was compared to the null model. The paired *t*-test was used to determine the effect of nest height change on predation experience. The difference in nest height among philopatric individuals, immigrants, and yearlings was tested with a likelihood ratio chi-squared test of GLMMs (Gaussian error, probit link function, and individual IDs as a random effect) and a chi-squared test of GLMMs (binomial error, logit link function, and individual ID as a random effect), to test the difference in predation rate among the three bird groups. In addition, the number of fledglings was compared with the likelihood ratio chi-squared test of GLMMs

(Poisson error, log link function, individual ID as a random effect). Gaussian error, probit link function, and individual ID as a random effect were also used to test the difference in the proportion of broadleaf trees in the territory among the three bird groups. To determine the factors affecting reproductive success (clutch size, brood size) of the Narcissus Flycatcher, and to compare the difference in reproductive success, a likelihood ratio chi-squared test of cumulative link mixed models (CLMMs), including philopatric status of males or the proportion of broadleaf trees in the territory, was used. In this case, the individual ID was a random factor, and both models were compared to the null model.

RESULTS

Trend of nest predation

The nest predation rate was only affected by nest height, and nests in a higher position above the ground were less likely to be depredated (Table 1, Fig. 1). The predation pressure was different between years, but the interaction of nest height and study years was not included in the final model, thus the trend on nest height did not significantly change between years (Table 1). In addition, no effect could be found for other nest site characteristics (nest site type, condition of the tree fragment with the cavity, DBH of nest tree) or forest construction.

Return rate

A total of 48.8% of the individuals returned to the territory when the previous reproduction had been successful. Only 38.1% of the individuals returned after reproductive failure (Fig. 2).

There was a significant effect of previous reproduction on the probability of return (GLMMs likelihood ratio chi-square test, null model vs. previous reproduction, $N = 62$, $\chi^2 = 52.645$, degrees of freedom (df) = 1, $P < 0.001$).

Nest site selection

When the nest was depredated in the previous year, philopatric individuals changed their next nest position higher (Fig. 3, paired *t*-test, $t = 7.287$, df = 5, $P < 0.001$). On the other hand, when the nest was successful, there was no tendency to change nest height between years (Fig. 2, paired *t*-test, $t = 0.104$, df = 6, $P = 0.920$). In total, philopatric mature individuals nested in a higher position than matured immigrants and first-breeding yearlings (Fig. 4, Table 2, GLMMs likelihood ratio chi-square test, $N = 59$, null model vs. philopatric status, $\chi^2 = 13.598$, df = 2, $P = 0.001$). Half of the yearling nests and 33% of the matured immigrant nests were depredated, but only 6.66% of philopatric matured male nests were depredated (Table 2), and the probability of nest predation of philopatric males was significantly lower than first-breeding yearlings and mature immigrants (GLMMs likelihood ratio chi-square test, $N = 58$, null model vs. philopatric status, $\chi^2 = 8.482$, df = 2, $P = 0.014$)

Clutch size and brood size

Individuals with high proportion of broadleaf tree in their territory had bigger clutch size (Fig. 5, GLMMs likelihood ratio chi-square test, $N = 41$, null vs. proportion of broadleaf trees, $\chi^2 = 5.002$, df = 1, $P = 0.025$) and bigger brood size (Fig. 5, GLMMs likelihood ratio chi-square test, $N = 32$, null vs. proportion of broadleaf trees, $\chi^2 = 5.414$, df = 1, $P = 0.019$). In addition, the proportions of broadleaf trees in the immigrants and yearlings territories were higher than that in the philopatric individuals and yearling territories (Fig. 6, GLMMs likelihood ratio chi-square test, N = 45, null vs. philopatric status, χ^2 = 6.352, df = 2, P = 0.042).

The clutch size and brood size of immigrants and yearlings were slightly bigger than that of philopatric individuals (Table 2), however, there was no significant difference (GLMMs likelihood ratio chi-square test, N = 40, null vs. philopatric status, χ^2 = 1.270, df = 2, P = 0.530). As for clutch size, the brood size for immigrants and yearlings was slightly bigger than in philopatric individuals (Table 2), although there was no significant difference (GLMMs likelihood ratio chi-square test, N = 30, null vs. philopatric status, χ^2 = 2.4028, df = 2, P = 0.301). Because of the nest predations, the average number of fledglings of philopatric individuals was bigger than that of yearlings and mature immigrants (Table 2).

DISCUSSION

In this study, the cost of dispersal to an unknown area and the benefit of philopatry in experience-dependent predation avoidance of the Narcissus Flycatcher were revealed. Within the study site, the Japanese marten *Martes melampus* and the Japanese rat snake *Elaphe climacophora* are the main predators of cavity nesters (Morimoto, unpublished, Okahisa, unpublished), thus, birds could avoid nest predation by nesting in high positions. Philopatric individuals accomplished improved nest site selection by nesting in high positions to escape from nest predation, especially after previous nest predation. On the other hand, immigrants and yearlings could not detect to the predation trend at the study site, and thus, they suffered from lower reproductive success. Furthermore, immigrants tended to nest in even lower positions than the first breeding yearling individuals. The prior experience of immigrants could not be determined, however, the slight decline in the tendency to return after reproductive failure suggests the immigrants might have been depredated in prior years, and changed their territory location. Thus, nesting in lower places might be caused by a difference of experience in nest predation; for example, higher nest predation rate at higher nest positioning. Nest predators of birds, i.e. crows, rodents, martens, and snakes, use different attack techniques (Walankiewicz 2002; Wesołowski 2002), thus, birds should collect accurate information of nest predation and adjust their nest site to local predation trends. In addition, in experience-biased nest site selection, the mismatch between the experience of immigrants and the predation trend at the current breeding site might cause reproductive failure.

The results suggest that the benefit of philopatry on nest predation avoidance is relative to the difficulty in assessing nest predation and the stability of nest predation trends. Abundant information is needed to make a suitable decision in each environment (i.e., different nest site availability, nest site structure, different predator species, and abundance of the predator). Any prediction of flexibility in response to the risk of nest predation assumes that birds can assess the predation risk somehow. Birds can assess predators through sighting, density of small rodents, vocalisation, and urine trail of predators, olfactory cues, faeces, chemical cues, and public information (reviewed by Lima 2009). In this study, the immigrants and yearlings could not assess the predation trend, while philopatric individuals could, especially when their nest had been previously depredated. This result suggests that the direct observation of nest predation would be the most informative aspect compared to other determinations (Lima 2009). Nest predation is never directly observed until they breed.

Therefore, the experience of defined areas might be generally beneficial for animals.

In addition, predators frequently occupy the same area for several years, and consistently forage in areas where they have previously been successful (Porneluzi 2003; Pöysä 2006). Few studies figured out that the predator has memory of specific locations and revisits similar locations, but it is clearly a reasonable assumption (Lima 2009). At the study site, high predation rates on lower nests did not change for 5 years, and thus, philopatric individuals adapted to the circumstances. But if the trend of predation was unstable between years, predation avoidance by experience might not be efficient. In addition, the benefit of escaping from an unsuitable habitat may compensate more than the cost of dispersal from an unstable environment. This suggestion is opposite to the general agreement that stable predation trends accelerate the dispersal of birds (Win-stay/lose-switch strategy: Switzer 1993, 1997).

Empirical studies support the win-stay/lose-switch decision-making of birds, for instance, the Ovenbird *Seiurus aurocapilla* is likely to disperse from the territory that experienced predation, because the territory that experiences predation in one year may be more likely to meet predation in the following years (Porneluzi 2003). The return rate decline of flycatchers after nest predation in this study means that some individuals chose lose-switch decision-making. The win-stay/lose-switch strategy is obviously beneficial when nest predation has a lethal effect on lifetime reproductive success of birds, and birds have no way to avoid the predation. However, when the birds can use the failure experience to improve reproduction, as seen here, and they can recover from a reproductive failure in their lifetime, birds can choose to remain in the depredated territory where predation has occurred. The results mean that the flycatchers that had failed in prior reproduction predicted their success in the next year, and thus they returned to the same territory. On the other hand, when they predicted the next failure, they dispersed. Hoover (2003) reported that when the Prothonotary Warbler *Protonotaria citrea* experienced nest failure, it tended to remain in its territory if its neighbourhood did not suffer nest predation. It is also known that the Black-legged Kittiwake *Rissa tridactyla* nested on better cliff were unlikely to abandon reproduction following nest predation (Danchin et al. 1998; Boulinier et al. 2008). These previous knowledge also suggests that birds predict the next breeding success by assessing the reproductive success of others, the nest site quality, and predation trend. In addition, this knowledge supports not only the win-stay/lose-switch strategy, but also that philopatry and site fidelity is available under stable predation circumstances. The exact cue for such decision-making of the Narcissus Flycatcher on remaining the depredated territory or dispersal could not be determined, but they might predict philopatry is better for enhancing reproductive success.

In some cases, older experienced males occupy better territories than younger ones in a breeding site (Potti & Montalvo 1991; Lundberg & Alatalo 1992; Mitrus 2006), while in this study, the clutch size and number of nestlings were only influenced by broadleaf tree density in the territory, and the clutch size was high in a broadleaf forest. In addition, the nest predation rate is not different among forest constructions. These results suggest that flycatchers could improve their fecundity with short dispersal from coniferous forest to broadleaf forest; however, the dispersal of breeding individuals in short distances has not been observed. Furthermore, immigrants and yearlings tended to occupy broadleaf forest where they can breed more nestlings, because of greater food abundance (Okahisa et al. 2014). These results suggest that philopatric individuals did not select a better area for increasing nestling number, but rather selected a familiar site to avoid nest predation. On the other hand, immigrants selected a better territory for increasing nestling number.

Some studies of decision-making in animals have described animal behaviour as being highly risk-sensitive, and the utility function of behaviour is based on a gain given the current state of wealth, rather than the overall wealth (dynamic utility function, Yoshimura et al. 2013). For example, the value of one egg is low when the individual is satiated, but high when the individual is starved of reproductive success. The results of this study suggest that immigrants might emigrate to another breeding territory after reproductive failure, and generally individuals in worse habitats tend to emigrate more often (reviewed by Matthysen 2012). Additionally, immigrants were likely to be starved of reproduction, in which case they might choose a better territory to increase the number of nestlings. On the other hand, philopatric birds might predict their reproductive success in the habitat, and the decision-making of bird philopatry was risk-sensitive and beneficial for philopatric individuals to sustain number of fledglings.

In conclusion, the Flycatchers could not comprehend a suitable nest site until the nest was depredated; therefore, a lack of experience in local nest predation was detrimental to them. These findings suggest that when birds can get information from local experiences, the always stay strategy can be beneficial.

Table 1 Model analysis of χ^2 compared with the deviance of the full model and the model without the factor (N = 60)

Factors	χ^2	df	P
Nest height	4.249	1	0.039
Nest type	0.020	2	0.990
Condition of the tree fragment	1.392	1	0.238
Diameter of breast height	0.375	1	0.541
Forest construction	1.231	1	0.267
Year	9.730	4	0.045
Nest height:Year	7.6632	4	0.105

Table 2 Nest failure and nest success of matured immigrants, matured philopatric individuals, and yearlings. Values for nest height, clutch size, and brood size indicate the mean ± standard deviation (SD). The average number of fledglings was calculated using the brood size and probability of a successful nest

	Matured philopatric individuals	Matured immigrants	Yearlings
N	18	12	30
Nest height	8.70±4.08	4.88±3.90	6.17±2.97
Probability of nest failure due to depredation	5.56%	40%	46.67%
Clutch size	4.46±0.78	4.63±0.51	4.58±0.61
Brood size	4.17±0.58	4.44±0.73	4.22±0.83
Average number of fledglings	3.935	2.733	2.252

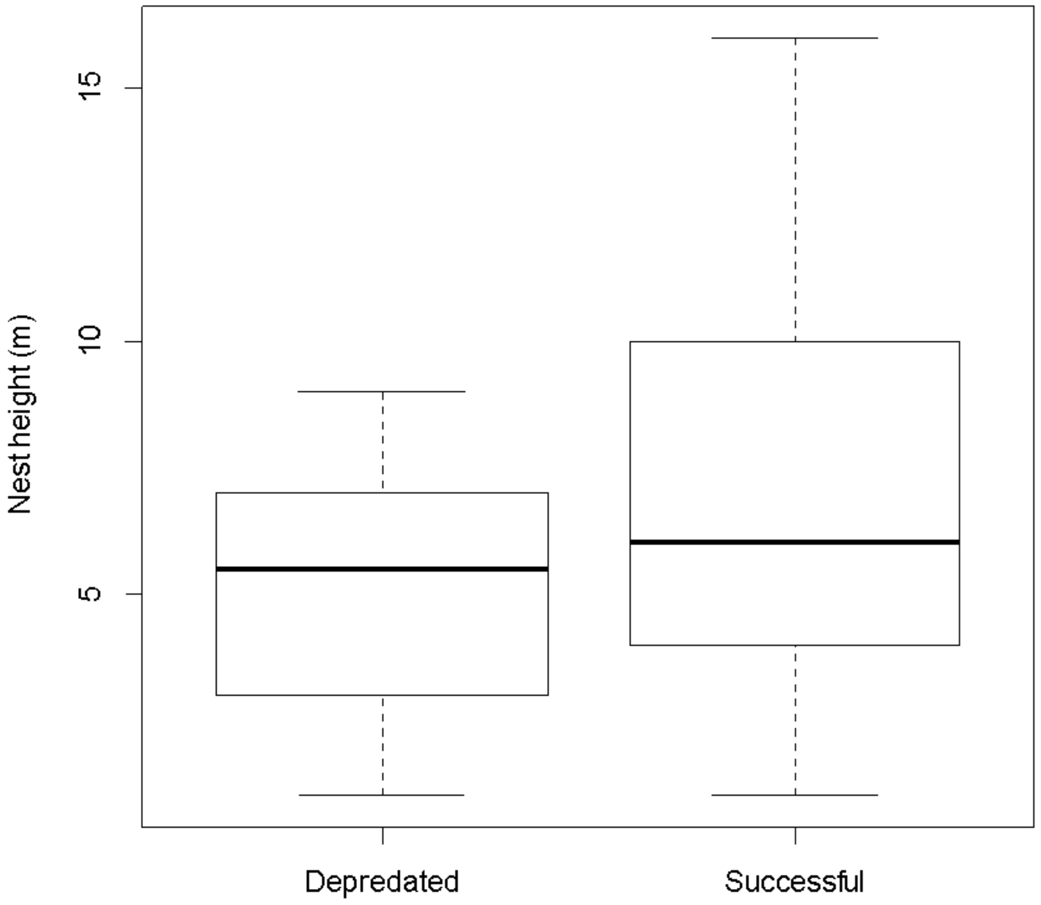


Figure 1. The nest height of successful and depredated nests. Thick horizontal lines represent medians, boxes represent upper and lower quartiles, and fine lines extending from boxes indicate extremes (maximum and minimum data 1.5 times the interquartile range, which is the distance between the lower and upper quartiles of the data)

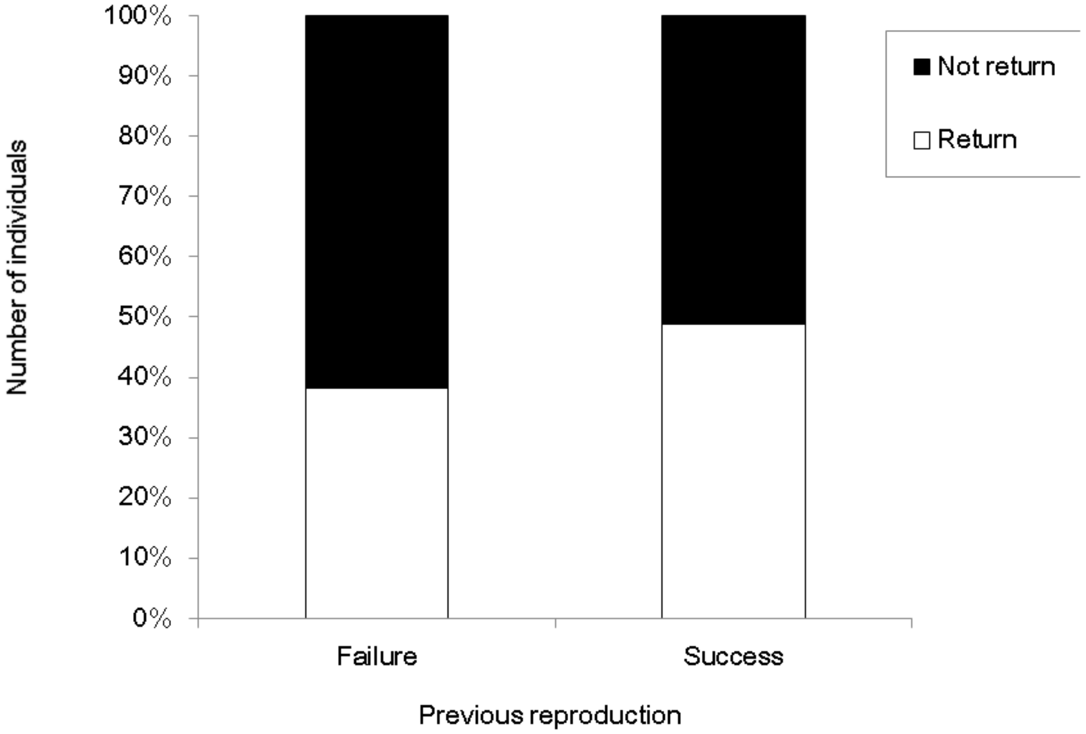


Figure 2. The number of philopatric individual and disappeared individual in relation to the previous reproduction.

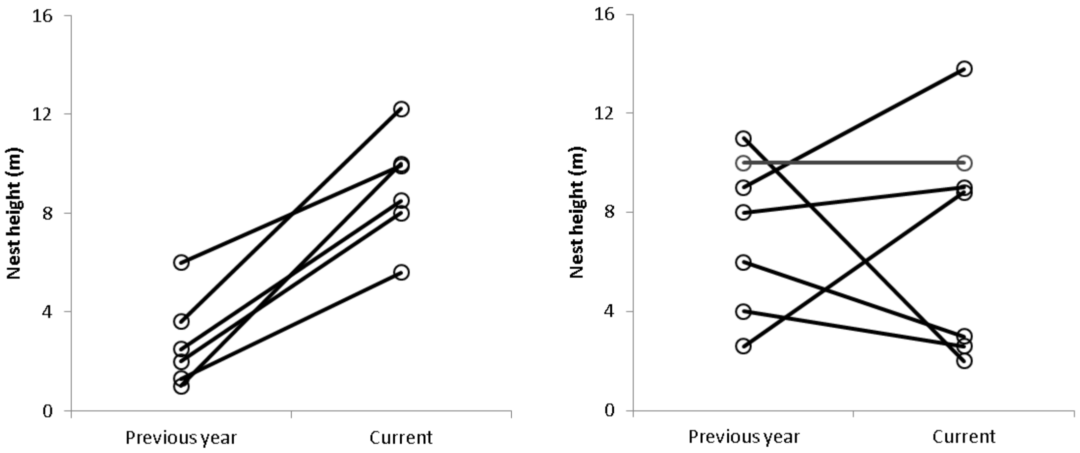


Figure 3. Nest height change between years when nest was depredated (left) or successful (right)

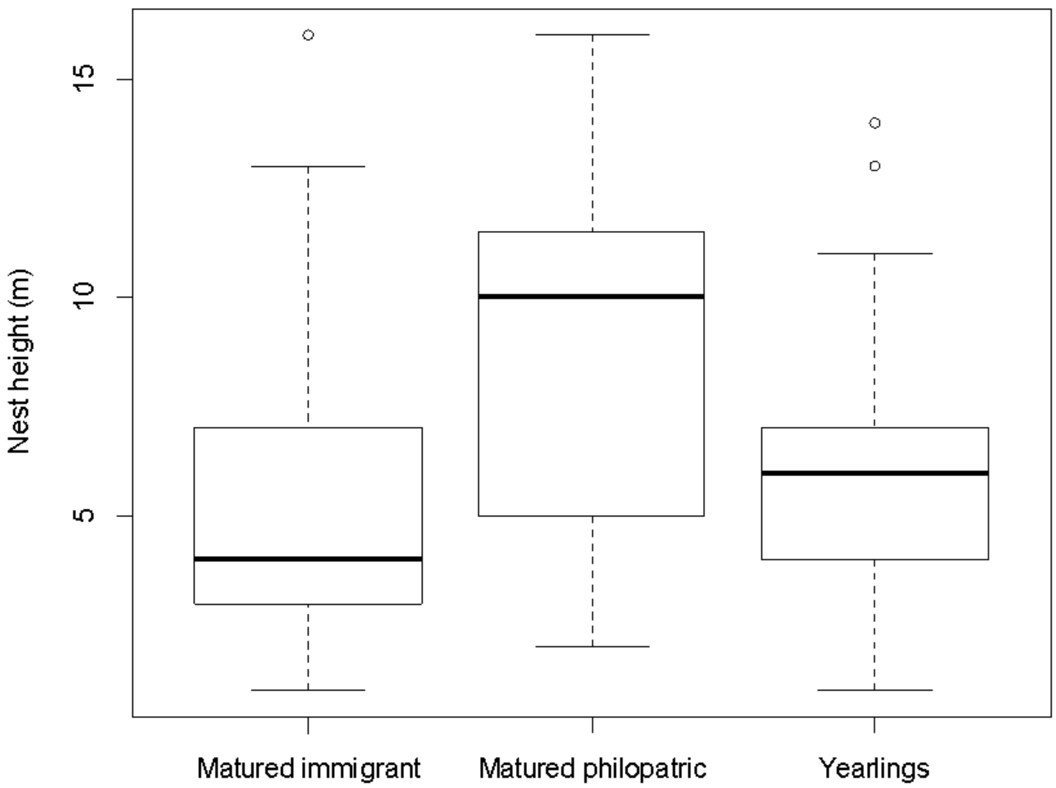


Figure 4. Nest height of matured immigrants, philopatric mature males, and yearlings. Thick horizontal lines represent medians, boxes represent upper and lower quartiles, and fine lines extending from boxes indicate extremes (maximum and minimum data 1.5 times the interquartile range, which is the distance between the lower and upper quartiles of the data). Small circles indicate outliers

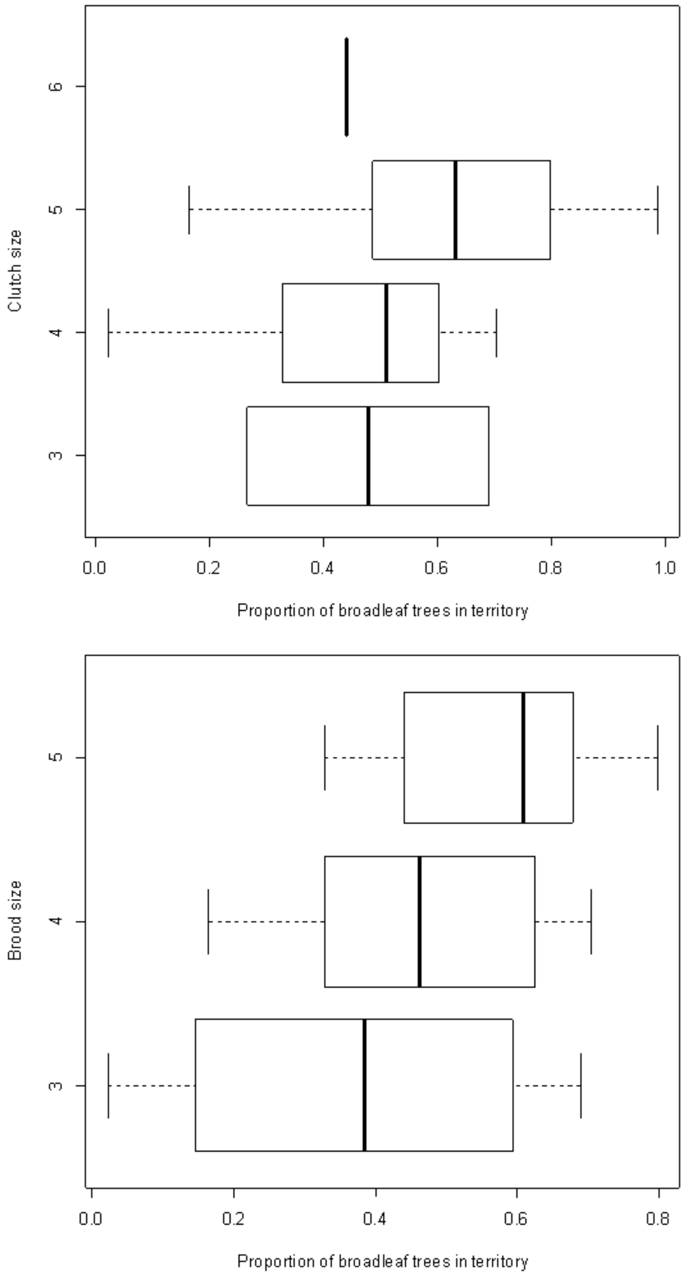


Figure 5. Clutch size and brood size in different densities of broadleaf trees in the territory. Thick horizontal lines represent medians, boxes represent upper and lower quartiles, and fine lines extending from boxes indicate extremes (maximum and minimum data 1.5 times the interquartile range, which is the distance between the lower and upper quartiles of the data). Small circles indicate outliers

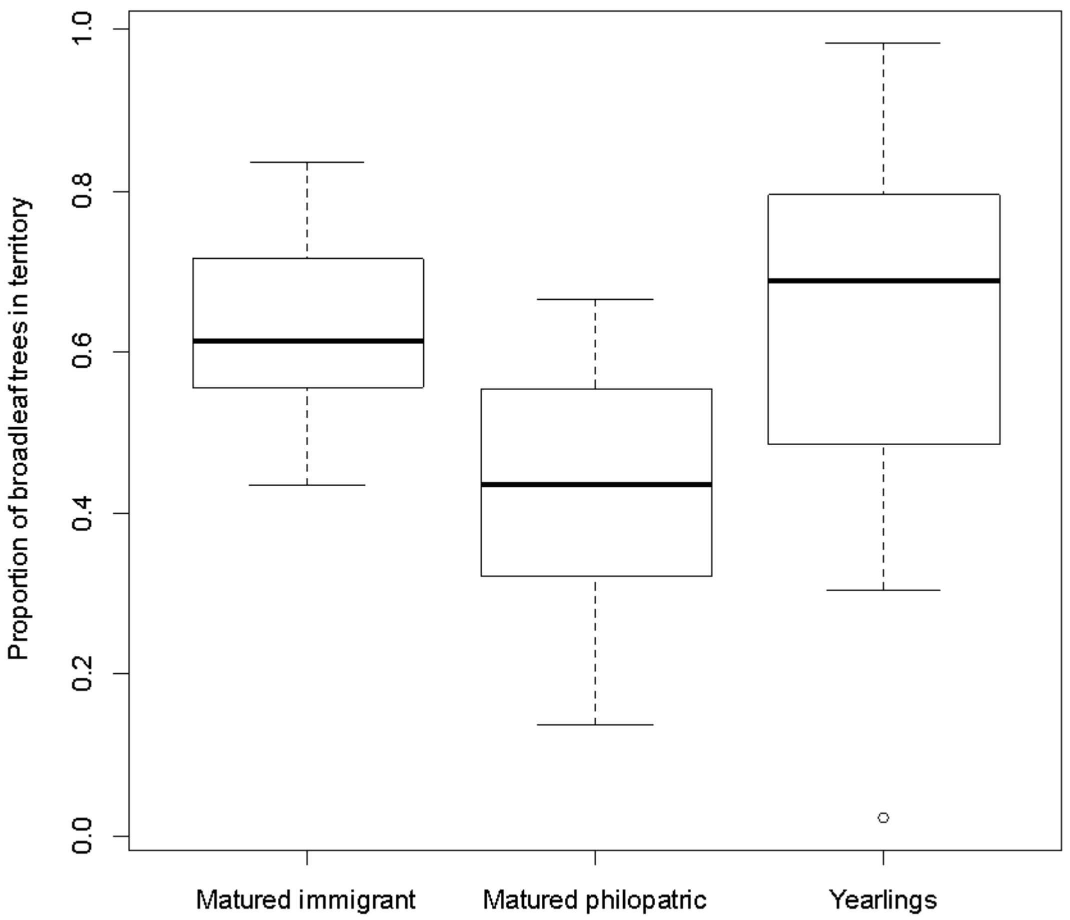
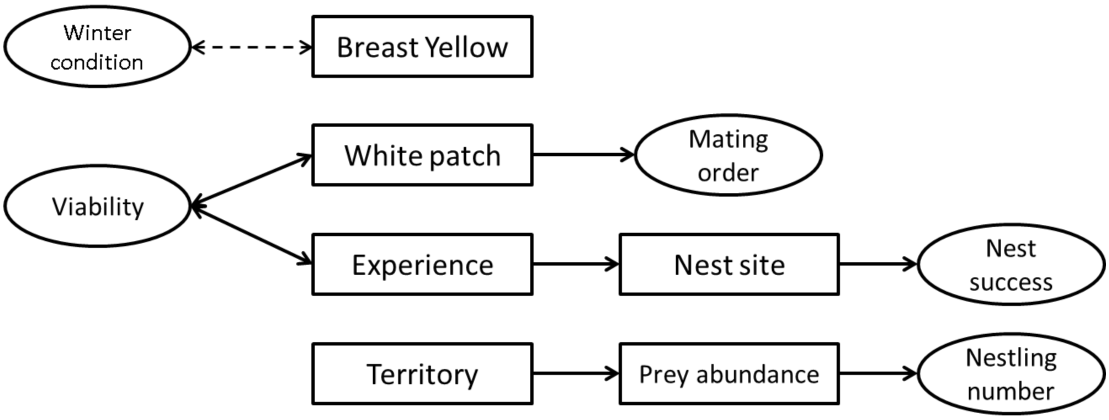


Figure 6. Proportion of broadleaf trees in the territory. Thick horizontal lines represent medians, boxes represent upper and lower quartiles, and fine lines extending from boxes indicate extremes (maximum and minimum data 1.5 times the interquartile range, which is the distance between the lower and upper quartiles of the data). Small circles indicate outliers.

DISCUSSION

(a) Mature male



(b) Yearling

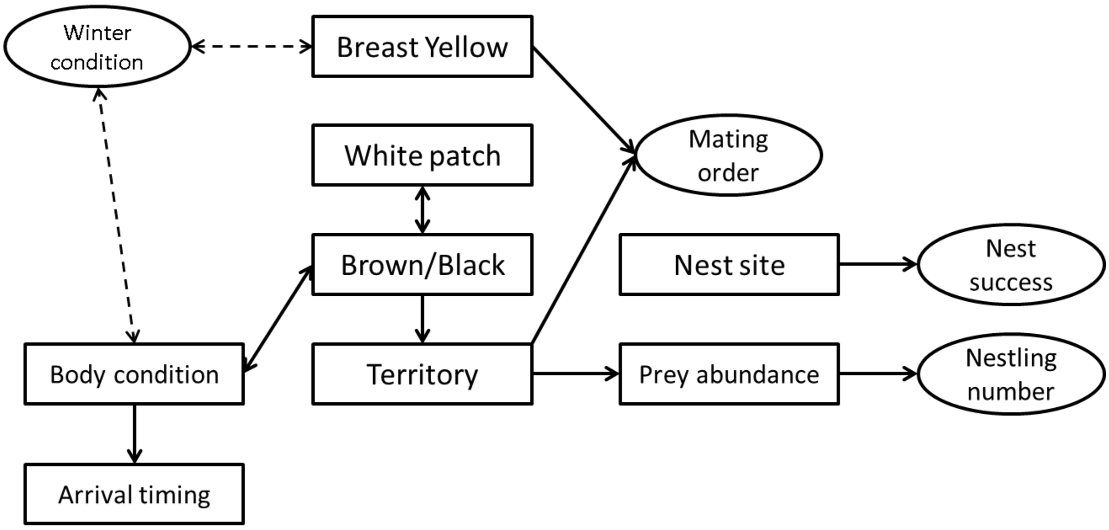


Figure 1. The flow chart of reproductive web in (a) mature and (b) yearling Narcissus Flycatchers. Solid lines indicate the correlations I figured out in this study, and the interrupted lines indicate the correlation I could not figure out but generally accepted.

Decision making for reproduction

In this desertion, I figured out (1) the detail breeding ecology of Narcissus Flycatcher, (2) information on their plumage (age and different time scale condition), (3) reproductive strategy, and (4) ecological function of the plumage colour in the sexual selections. These results allow us describing the reproductive ecology web of Narcissus Flycatchers (Fig. 1).

The reproductive strategy was different between mature and yearling males. The prey abundance in territory was more important for yearlings, but the mature males return same territory for getting higher proportion of nest success because of their adequate nest site selection by experience.

In addition, the plumage color had function for signalling difference of male strategy. Interestingly, female mated with mature male focused on white patch size which indicates male viability and condition in previous breeding area. The female decision was beneficial to get higher property of nest success because the elder male had experience for enhancing adequate nest site selection.

In contrast, yearling male meets trade-off and competition to obtain better territory with abundant prey. Female having mated with yearling also focused on their territory and direct benefit for increasing nestling number and clutch size. However they did not pay attention to white patch size and delayed plumage maturation itself. This is probably because the two traits could not reliable signal for female because the white patch obviously could not reflect the viability and prior condition of yearling. Therefore the male strategy, plumage function and female decision making of flycatchers strongly connected with each other. These results have several breaks through points.

Multiple message

The white patch size is important for the mature male for attracting female; however, breast yellow is important for yearling male for attracting female. These results indicate that the different male trait had same function in a different context and the messages of male traits were different. Thus, our results strongly support multiple message hypothesis （Møller and Pomiankowski 1993, Johnstone 1996). Several studies argued different pigmentations were likely to convey different messages (Hill & Montgomerie 1994, Linville & Breitwisch 1997, Olson & Owens 1998, McGraw & Hill, 2000). Beyond this, our result indicates there is different male strategy, and females make decisions by using different information in different context (mature male or yearling).

The findings (1） the Narcissus Flycatcher had life history traits which are adaptive to nest predation (the shortest incubation, nestling stage, and the longest feeding for fledgling in the genus *Ficedula*), (2) male could enhance nest site selection by experience of predation to increase reproduction, (3) white patch of male indicates viability and condition in previous breeding season, (4) female focused on white patches on mature male rather than breast yellow and territory quality, means a white patch is the reliable signal of male viability and experience, and female decision is beneficial because of reproductive enhancement by the male experience for nest predation avoidance. Kokko and Lindström (1996) predicted using a mathematical simulation that the female mate preferences for elder males evolved by female preference for the genetic quality of viability. In addition to the genetic benefit, our results indicate there was a direct benefit for selecting elder males because of their experience. I could not reveal why female could adequate choose in this study. While, the fact that improvement of nest site selection is plastic change rather than instinctive behavior suggests the benefit of female decision on male white patch might vary in environment.

Thus, strength of female choice on the traits may be different between regions, similar to the Pied Flycatcher (see Alatalo and Lundberg 1992). There would be other regions having different predation pressure, in such region the message of the white patch may not include individuals' experience on predation avoidance. Until now, reproductive enhancements with ages are already reported in several species; thus, even when the context of benefit of male experience are different, the reproductive enhancements may be acceptable in general. Comparative study will be needed.

In contrast, the findings (1) yearling made inadequate nest site choice thus nests were often depredated, (2) yearlings moulted many feathers in wintering area occupied territory with abundant prey, (3) moulting many feather decrease male condition, (4) female chose yearling in territory with abundant prey indicate that yearling could not avoid nest predation because of the lack of experience, but they can increase nestling number by occupying the good territory. Females also focus on prey abundance when they mate with yearling male to increase nestling number. The decisions of yearlings and females mating with them seemed like high-risk high-return strategy. The flycatchers could not select nest site adequately because of their lack of experience; thus the strategy focusing on the benefit when they success is beneficial to increase reproduction in a year, or yearlings were just trapped by predators. In addition, the male flycatcher could construct feather with wider white patch in territories with more abundant prey, and female focused on the white patch on mature male. Thus, the territory selection of yearling male might be also beneficial for increasing future female attractiveness and lifetime reproductive success.

Combination of multiple trait

I found out not only the multiple messages on different pigmentations, but also the hierarchical use of messages on plumage characteristics. As I firstly predicted, the result is probably affected by delayed plumage maturation. The yearling expressed only some ornamentations; thus the female should have used different cues. The function of trait's combination was scarcely studied (Candolin 2003, Hebets and Papaj 2005). Thus, the result of this desertion giving a great knowledge of plumage function in birds.

Multiple receivers

In addition to the different function in a different context, in inter-sexual selection, the brown and black feather had the significant effect in inter-sexual selection. Thus, the result supports multiple receivers hypothesis (Pryke et al. 2001, Andersson et al. 2002, Guindre-Parker et al. 2013) in this case, the different traits functioned in different relationships between males and females. The multiple receivers hypothesis was supported by several studies (e.g., van Dongen and Mulder 2007, 2009 Guindre-Parker et al. 2012). The biggest difference between our study and such previous studies was that only yearling of Narcissus Flycatcher had brown plumage, and I could not find any plumage effect on male territory in mature male. Thus, the multiple receiver hypothesis is acceptable only for delayed plumage maturation of yearlings.

A function of delayed plumage maturation is escaping from strong male-male competition (status signaling: e.g. Hill 1989, Morimoto et al. 2006, reviewed by Hawkins et al. 2012), thus the multiple receiver hypothesis might be accepted in bird species having delayed plumage maturation.

DPM and evolution

The clearly different reproductive strategy and selection pressures on mature and yearling male were central discussion point for the evolution of delayed plumage maturation and evolution of plumage color in the flycatcher. The breast yellow patch and brown/black feathers were important for yearlings. There was no difference on yellow patch color between mature and yearling male. This indicates yearling does not have delayed plumage maturation on this part. In other word, yearling male already evolved their breast plumage sufficiently for attracting female because of the pressure caused by female mate choice. In addition, there was the wide variety of breast yellow plumage in males. Thus the carotenoid yellow is now reliable signal for Narcissus Flycatcher.

On the other hand, having more black feathers is beneficial for occupying better territory; thus it might be beneficial for the yearling male to evolve to have more black feathers. While yearling male suspend brown feathers and the numbers of brown feathers varied between individuals. This is probably because the trade-off between arrival condition and winter moulting. Moulting more feathers caused worse condition and the worse condition cause later arrival to breeding site (Okahisa et al. 2013). Thus, the delayed plumage maturation of the flycatcher is a result of the trade-off rather than evolution under other adoptive mechanisms (status signal, female mimicry, Hill, Hadfield). The fact that even second summer plumage male did not express complete pure black feather in tibial feathers also support the larger cost of winter moulting.

The white patch of yearling had no effect in the male-male interaction and female mate choice, thus expressing white patch is not beneficial for yearlings. The reason why some yearlings express is not clear, while there is a correlation between white patch size and number of moulting feathers in yearlings. Thus because of the benefit of winter moulting and genetic correlation, yearling might wear some white patch.

In contrast, there was a benefit for the mature male to wear larger white patch. If there is not big cost for wearing wider white patch, larger white patch rapidly evolve for the sake of attracting female. The condition dependence and reliability of white pigmentation are still ongoing issues (see Török 2003, Guindre-Parker et al. 2013), because larger white patch means less melanin based-black part, thus bearing cost would be smaller than others (Török 2003 see also Badyaev and Hill 2000). Thus focusing on the depigmented white patch can be important for revealing the evolution of the flycatcher. Studies treating regional and populational difference will be needed.

Conclusion

Here the detail function of plumage and connections between ecology of Narcissus Flycatcher were figured out. The knowledge on the association between plumage function and ecology is crucial for revealing the evolution of bird plumages. However experimental study and phylogenetic study will be needed in the next step. In addition, this, Narcissus Flycatcher is the best material for figuring out the trade-off of moulting and breeding; thus comparative study of different subspecies having different morphology and moulting strategy is important for the revealing evolution of moulting and breeding strategy of birds.

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和文要旨

題目：キビタキの羽色の機能

鳥類の明瞭な性的二型と雄の羽色の個体差は性選択という着眼点に基づいて古くから活発に研究されている。近年、ある鳥の持つ黄色、黒色、白色などといった異なる色彩が個体の質という情報を伝達するための類似した補助信号として機能するのか（Back up signal hypothesis）、それとも文脈に応じて個別の羽色が独立的に機能する複数情報信号なのか（Multiple message hypothesis）が注目されている。だが、こうした観点から羽色の機能を解明する取り組みは少なく、いまだ一般論が確立されていない。

そこで本研究では長期的な野外調査に基づいて、渡り鳥キビタキ *Ficedula narcissina* の生活史を解明し、キビタキの羽色の加齢による個体内変異および発現に伴うトレードオフを解明する。さらに、同性間性選択および異性間性選択における羽色の機能を解明することによって、キビタキの持つ複数の羽色が補助信号なのか複数情報信号なのかを検討する。

1 章:キビタキの生活史形質　対象生物キビタキは世界で最も研究されている *Ficedula* 属の鳥種でありながら、生態が未知であることから、本章では山梨県富士山原始林においてキビタキの詳細な繁殖生態を解明し、行動生態学的材料としてのキビタキの特性を検討した。キビタキは完全な一夫一妻であり、入口の広い開放的な樹洞という他の鳥類に見られない特殊な環境を営巣場所として選択していた。また、同属の鳥類と比較して、抱卵日数・育雛日数が最も短かった。こうした繁殖戦略は鳥類の生活史においてもっとも危険な営巣という段階を早く終える適応であることから、キビタキの生活史は巣における高い捕食圧のもとで進化してきたと考えられる。さらに、雄が羽色を雌に見せ付ける飛翔とダン

スによるディスプレイを行うこと、激しく互いの羽を攻撃しあう雄同士の闘争行動が発見された。これらはキビタキの社会に羽色が機能することを示唆する。

2章：加齢に伴う形態の変化　生物では一般に加齢に伴う形態変化が認められ、ヒトによって検出可能な形態の変化は対象種の中でも認知されている可能性が高い。そこで、キビタキの体サイズ、羽色、虹彩色が加齢に伴ってどのように変化するかを検討し、生態研究において重要な要因である個体の年齢を査定する手法を開発した。キビタキを捕獲・標識し、加齢に伴う個体の形態の経年変化を記載した。キビタキの雄は翼長・尾長・虹彩色・脛羽が1歳齢、2歳齢、3歳齢以上の集団によって異なっており、2歳齢まで褐色の羽をもつという特徴から識別できることが明らかとなった。こうした成熟遅延は種内で認知されている可能性がある。

3章：羽色が伝達する異なる情報　鳥類の持つ複数の羽色が補助信号なのか複数信号かは、複数の羽色が独立な挙動を示すか、同調した挙動を示すかによって検討することができる。これは類似する情報を伝達する場合には羽色が類似した挙動を示すためである。そこで、キビタキのカロテノイド由来の喉と腰の黄色、メラニン由来の黒色と褐色、ケラチンのみによって発現される白色の羽について、羽色の挙動の相関、加齢による変化、換羽期に占めていた縄張りの質との関係を検討した。その結果、キビタキの白色の大きさは個体内変化が小さく、集団としては加齢とともに大きくなる傾向にあった。一方、カロテノイド由来の喉の黄色・腰の黄色は個体内変化が極めて大きかった。また、すべての羽色は相関しなかった。これにより、白色は生存力の高さを示す一方、黄色は個体のコンディションを示し、キビタキの羽色が異なる情報を伝達する複数信号として機能しうることが示唆された。

4章：同性間性選択における羽色の機能　成熟遅延の認められる黒色と褐色の羽色が雄

間闘争において、雄の強さと弱さを示す信号として機能するとの仮説を立て、雄間闘争の直接観察によってこれを検証した。その結果、侵入者が広い褐色部を持つ場合には直接的な攻撃行動を伴った闘争は起こりづらく、侵入者が広い黒色部を持つ場合には雄間闘争は直接的な闘争に発展する確率が高かった。また、褐色を持つ侵入者は闘争の勝率が低い一方、黒色部の広い侵入者は闘争に勝利しやすかった。これらは褐色部の広さが雄の闘争における弱さを示し、雄間闘争における負傷や死亡の危険を回避するための地位伝達信号として機能することを示している。

5 章 : 異性間性選択と複数受信者仮説　色彩性的二型は異性間性選択によって進化したと一般に考えられている。そこで、雌による異性間性選択におけるキビタキの羽色の機能を解明するために、本章では雌とつがいになる順序に対する雄の形態の影響を検討した。その結果、成鳥の雄では翼の白斑が大きい個体ほど雌と早く番っていた。一方、若鳥では餌量の多い縄張りを獲得し、喉が赤みを帯びている個体が雌と早く番っていた。これはキビタキの雌が雄の成熟遅延を認知することで選択性を変化させていることを示唆する。また、前章の雄間闘争において機能した黒色と褐色の程度は機能しなかった。そのため、キビタキの羽色は同性間と異性間という異なる関係において、独立的な選択圧を受けていると考えられた。

6 章 : キビタキの成鳥と若鳥の異なる繁殖戦略　前章において、雌が雄の年齢に応じて性選択を変化させた。これは若鳥と成鳥の雄が異なる繁殖戦略をもつことによって、雌にとっての利益が雄の齢によって変化することを示唆する結果である。そこで、若鳥と成鳥の雄の繁殖戦略を検証した。その結果、キビタキの雄は縄張りに対する固執性が強く、成鳥は同じなわばりに留まり、巣の捕食を回避しているのに対して、若鳥は餌量の多い環境で多くの雛を育てるという選択を行っていることが示された。

一連の結果は、キビタキの持つ黄色・黒色・白色が異なる齢・コンディションに対する感受性を有し、羽色によって異なる受信者がおり、さらに文脈によって機能する羽色が異なるという Multiple message hypothesis/ Multiple receiver hypothesis を支持した。

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