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Breeding timing and nest predation rate of sympatric scops owls with different dietary niche breadth

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Abstract

Breeding timing is one of the key life history traits considered to be under strong stabilizing selection, such that offspring should be born when food resources are most abundant. Predation, however, may also affect the breeding timing because nest predation is a leading mortality for many species, although this possibility has been less considered. Here, we examined the possible effects of nest predation on breeding timing by comparing sympatric scops owls in a subtropical forest where only reptilian predators are present. The Japanese Scops Owl (*Otus semitorques* Temminck and Schlegel, 1850), a dietary generalist, bred one month earlier than the specialist Ryukyu Scops Owl (*Otus elegans* Cassin, 1952). The breeding timing of the Ryukyu Scops Owl matched with the emergence of their main prey species, but also matched with predator activity. Accordingly, the predation rate on eggs or nestlings was 7.5 times higher in the Ryukyu Scops Owl (13.9%, 21 out of 150 nests) than in the Japanese Scops Owl (1.9%, one out of 52 nests). Clutch size, on the other hand, was significantly larger in the Ryukyu Scops Owl than in Japanese Scops Owl, possibly compensating loss from predation. Although alternative explanations still remain, our results suggest that the food generalist might have adjusted its breeding timing to avoid nest predation, whereas the breeding timing of the specialist might have been constrained by the availability of its main prey items.

Key words: breeding timing, nest predation, dietary breadth, scops owl, *Otus elegans*, *Otus semitorques*, snake predation.

Introduction

Breeding timing, including mating, egg-laying, and hatching, is a key life history trait, and is considered to be under strong stabilizing selection, such that offspring should be born when food resources are most abundant (Daan et al. 1990; Houston and McNamara 1999). This is supported in many organisms, including insects (Kennish 1997), fishes (Clifton 1995), reptiles (Lichtenbelt and Albers 1993), birds (Lack 1954; Perrins 1970), and mammals (Bunnell 1980). Adaptation to food availability may be more prominent in arctic or temperate regions because seasonality and resource synchrony are stronger than in tropical areas (Perrins 1970; Price et al. 1988; Visser et al. 2004).

Breeding timing, however, may also be affected by other factors. Predation pressure potentially influences breeding timing because predation in early life stages is the leading cause of mortality in many organisms (Ricklefs 1969; Frank and Leggett 1982; Morgan 1992; Sih and Moore 1993; Martin 1995; Chivers et al. 2001). In amphibians, breeding phenology might shift to reduce predation pressure by reductions or increases in developmental timing depending on predator species (Sih and Moore 1993; Warkentin 2000; Anderson and Petranka 2003). Another well-known strategy for predation avoidance is reproductive synchrony among conspecific individuals (Ims 1990), by which predation capacity becomes satiated and, therefore, per capita survival increases (Spencer et al. 2001; Christy 2003). This phenomenon is generally observed in small prey, such as insects and gastropods (Christy 2003), but is also found in marine turtles (Carr and Hirth 1961; Spencer et al. 2001) and some birds (Gochfeld 1980; Westneat 1992). Some plants exhibit a more extreme form of synchronicity, whereby many different species produce seeds or fruits at the same time once every several years

(Silvertown 1980; Kelly and Sork 2002). However, a presumably more simple adaptation, the shift of breeding timing away from seasons of predator activity, has been rarely reported. A few studies in birds, specifically testing for the possibility, showed weak evidence (Morton et al. 1972; Wiklund 1984; Young 1994; Preston and Rotenberry 2006).

Supportive evidence for shifts in reproductive timing for predation avoidance may be lacking (1) because most studies have been conducted in higher latitudes where food availability is pulse-like, and therefore the importance of food phenology outweighs predator avoidance or (2) because different predators are present for a given species, and therefore adaptation to multiple predators with different predation timings may be impossible. Thus, we expected that timing shifts are more likely to occur (1) in tropical or sub-tropical regions where seasonality is less apparent and food sources are not limited to a specific season and (2) in systems where only a few predator species exist. In addition, we also postulated that (3) shifts in breeding timing due to predation avoidance may be more possible in dietary generalists rather than specialists, because generalists can exploit different prey items in different seasons.

Comparing populations with and without predators should provide a direct assessment about whether adaptation of breeding timing occurs against predation pressure. However, such contrasting sites do not always exist in natural systems. Comparative studies between closely related species provide indirect evidence for correlation studies (e.g. Hilton et al. 2000; Palacios and Martin 2006), although there are some potential caveats, such as different evolutionary histories (Garland and Adolph 1994). As a first step, we employed a comparative approach to infer the potential effects of food availability and nest predation on breeding timing.

Scops owls on Okinawa Island, in the southernmost archipelago of Japan, are suitable for examining the above predictions. First, because of the comparatively weak seasonality on this subtropical island, resource availability may not strongly be constrained to a limited season, possibly allowing owls to change their breeding timing to avoid predator activity. Second, predation avoidance may be relatively easy for owls, because snakes are the only predators of their eggs and nestlings. Third, dietary generalist and specialist congeneric owls occur syntopically throughout the year (i.e., residents). The Japanese Scops Owls (*Otus semitorques* Temminck and Schlegel, 1850, hereafter called JSO) preys on various taxonomic groups (e.g., insects, centipedes, birds, small mammals, and reptiles), whereas the Ryukyu Scops Owl (*Otus elegans* Cassin, 1852, hereafter called RSO) feeds predominantly on orthopterans (about 80% of their diet) (Toyama and Saitoh 2011). As the two species are rather similar, belonging to the same genus and having similar body sizes (JSO: 24 cm, RSO: 20 cm), but have different diets, we can compare the effect of dietary niche breadth on the flexibility of reproductive timing. To examine the effects of nest predation on breeding timing we monitored the reproductive parameters of these syntopic scops owls by setting a large number of nest boxes (up to 300) over 5 years.

Material and methods

Study site

We conducted field investigations between 2004 and 2008 in a sub-tropical forest located in Kunigami Village, northern Okinawa Island, Japan (26°45'N, 128°12'E). Our core study sites were the Yona experimental forest of the University of the Ryukyus (318 ha) and the Kunigami forest park and outskirts (about 100 ha). We investigated the

reproductive biology of the two scops owls, i.e., Japanese Scops Owl (JSO) and Ryukyu Scops Owl (RSO), in natural tree cavities (JSO: $n = 10$, RSO: $n = 17$) and nest boxes (JSO: $n = 43$, RSO: $n = 133$). The total numbers of broods observed were 53 and 150 for JSO and RSO, respectively, but sample sizes differed among parameters, such as reproductive timing, clutch size and predation rate, because some were not measured in the field.

The forest in Kunigami Village is secondary forest, consisting of evergreen broad-leaved trees (e.g., *Castanopsis cuspidata*, *Quercus miyagii*, and *Trema orientalis*). The forest floor is covered with ferns and fallen leaves. The area is dominated by the Asian monsoon climate, which is characterized by high temperatures (mean annual temperature: 20.0°C) and high precipitation (mean annual rainfall: ~ 2400 mm), most of which occurs from May to August. Insects are present in the forest throughout the year, although some species emerge in spring. In winter, many small birds migrate to the island. Owls and snakes are the top predators in the forest, because no large mammalian or raptorial predators are present (Takagi 2009). Although there are some raptor species that are slightly larger than the scops owls, such as the Japanese Sparrowhawk *Accipiter gularis* (27 cm, diurnal species) and the Brown Hawk Owl *Ninox scutulata* (30 cm, nocturnal species), they do not attack scops owl's nests (Toyama pers. Obs.): they prey mainly on small birds, rodents and insects (Hirano and Kimijima 1992; Toyama, unpubl data).

Nest boxes

Nest boxes of two different sizes were used. A large nest box (entrance: 10 cm in diameter, bottom: 25 × 25 cm, depth: 30 cm) was designed for JSO, based on those

used on Honshu, the main island of Japan (Iida 2001). A small nest box (entrance: 6.5 cm in diameter, bottom: 15 × 15 cm, depth: 30 cm) was designed for RSO, based on the size of Okinawan woodpecker nests, because RSO frequently use old Okinawan woodpecker nest-holes (M. Toyama, unpubl data). Thirty small nest boxes were set in 2004 and 2005, and 150 small and 150 large nest boxes were set in 2006, 2007, and 2008. These boxes were set at three different heights (low: < 2 m; middle: 3–4 m; high: 7–12 m) to examine nest site preferences, but this was not the focus of the present study. All nest boxes were cleaned and reestablished on randomly selected trees every year during December - January well in advance of the breeding seasons of these owl species (i.e. March-July).

Breeding parameters of scops owls

Natural cavity nests and nest boxes were monitored using CCD camera equipment specifically designed for tree cavity monitoring (Matsuoka 2002). Breeding timing, clutch size, number of fledglings, nesting success (i.e., the proportion of nests that successfully fledged at least one offspring), predation rate, and the causes of reproductive failures were recorded. The CCD camera monitoring of each nest was completed within five minutes to minimize observer disturbance, and was conducted at least twice a week from late March to mid July to cover the entire breeding season. Since breeding timing, clutch size, number of fledglings, nesting success, and predation rate were not significantly different between natural cavity nests ($n = 7-10$ and $12-17$ for JSO and RSO, respectively) and nest boxes ($n = 42-43$ and $118-133$ for JSO and RSO, respectively) in either owl species (Mann-Whitney-Wilcoxon test and Fisher's exact test, $P > 0.10$), we pooled data for subsequent analyses. In addition, these parameters

were not significantly different between years (Kruskal-Wallis test and Fishers's exact test, $P > 0.05$) except for breeding timing. Therefore, we also pooled the yearly data except for breeding timing. We did not identify individuals by color rings because capturing adults or fledglings during breeding may lead to nest abandonment. Therefore, the proportions of pairs breeding consecutive years are unknown.

Breeding timing was determined both directly and indirectly. The date when nestlings left their nests (i.e., the end of breeding) could be directly assessed because each nest was monitored every other day during the nestling leaving period; therefore, the maximum possible error was one day. The date of initiation of egg-laying (i.e., the start of breeding), on the other hand, was estimated based on the nestling leaving date and on several cases of direct observation (i.e., we observed first egg directly by CCD camera monitoring). The exact date of egg-laying was difficult to determine because eggs were not observed when females sat on nests. In addition, scops owls are very nervous at the beginning of their breeding seasons and might abandon breeding due to observation disturbance. Therefore, we reduced the frequency of CCD monitoring to every 3–4 days around the beginning of the breeding season. As a result, only three and seven direct observations were made for JSO and RSO, respectively. The average period between egg-laying and fledglings leaving (62.5 days for JSO, range 61–64 days; 57.8 days for RSO, range 55–62 days) was used to estimate the start of breeding for each nest. As the periods directly observed were within the range of other RSO populations (Severinghaus 1989) and the variation among nests was comparatively small, we considered the bias resulting from individual variations to be minimal and to not have a significant effect on our results. The date of hatching was assumed to be the middle date between egg-laying and fledgling leaving dates, based on observations of other scops

owls (Severinghaus 1989; Gelhebach 1994).

Causes of nesting failure were categorized into the following four categories: predation by snakes, predation by unknown predator, unhatched eggs, and other. Direct observation of snakes in owl nests was regarded as nest predation by snake. The loss of all or some eggs or nestlings with the disappearance of the female was regarded as predation by an unknown predator (only female incubate eggs and nestlings in the scops owls). Unhatched eggs were recorded where females incubated their clutch for at least three weeks but eggs were not hatched and females left their nests. Other causes of failure followed rare accidents such as nest disturbance by humans (e.g., amateur photographers), nest destruction due to a typhoon, nest site competition with Brown Hawk Owls, and death of the female in the nest box.

Seasonal changes in snake activity

Since snake predation, especially by the Ryukyu Odd-tooth Snake *Dinodon semicarinatum*, was the main cause of nesting failure (see Results), we monitored snake activity during the owl breeding seasons. Snake activity is strongly affected by ambient temperature (Gibbons and Semlitsch 1987). Thus, the relationship between snake activity and temperature was established. We drove a car along a paved forest road (8 km) close to our study sites at a speed of 15 km / h and counted the number of snakes on the road. The survey was conducted during night-time when snakes are more active. We identified all the snakes observed (Ryuku Odd-tooth Snake, Okinawan Habu *Protobothrops flavoviridis*, and Ryukyu green Snake *Cyclophiops semicariatus*) because all species can be a potential predator. Ambient temperature was also recorded. The road census was conducted 2.5 times a week on average (33 times in total) between 9 April

and 1 July 2007. To estimate relative snake activity, we constructed a generalized linear model (GLM) with a Poisson distribution and a log link function. Number of snakes counted was used as a response variable and the ambient temperature at the time was used as an explanatory variable. This relationship was then used to estimate relative snake activity throughout owl breeding seasons, using daily temperature data collected by the Oku observation station of the Meteorological Bureau of Japan, located about 10 km north of the study site. We used daily minimum temperature, instead of daily average temperature, because the snakes are nocturnal (Uchiyama et.al. 2002).

Statistical analyses

Differences in breeding timing (fledgling leaving dates), clutch size, and number of fledglings were compared between species using Mann-Whitney-Wilcoxon test. Fisher's exact probability test was used to examine differences in nesting success and nest predation rate between the species. All the analyses, including GLM, were carried out by the R software package (ver.2. 12. 0, R Development Core Team)

Results

Breeding timing

Timing of breeding in JSO was monitored for 50 nests during 2006-2008, whereas that in RSO was monitored for 113 nests during 2004-2008. Breeding timing of RSO was significantly different among years (Kruskal-Wallis test: $df = 4$, $\chi^2 = 21.9$, $P < 0.0001$), but not for JSO (Kruskal-Wallis test: $df = 2$, $\chi^2 = 5.1$, $P = 0.07$). Breeding timing of RSO was delayed in 2005, although no clear difference was observed for other years.

The generalist, JSO, bred one month earlier than the specialist RSO for all the years studied (Fig. 1; Mann-Whitney-Wilcoxon test: $P < 0.00001$). JSO laid eggs between early March and April (Mean \pm SD: 17-March \pm 6.9 days; Fig. 1) and their nestlings fledged between early May and early June. RSO, on the other hand, laid eggs between late April and mid-May (Mean \pm SD: 08-May \pm 6.3 days; Fig. 1) and their nestlings fledged between late June and mid-July (Fig. 1).

Breeding success

Clutch size was determined for 51 and 130 nests of JSO and RSO during 2004-2008, respectively (Fig. 2a), whereas the number of fledglings for 52 and 141 nests of JSO and RSO, respectively (Fig. 2b). In addition, we occasionally observed other cases of successful nesting (i.e. at least one fledging), amounting to one case in JSO and nine cases in RSO, respectively, although the exact number of fledglings was not determined because females remained in the nests. Thus, the breeding success of JSO and RSO was calculated based on 53 and 150 nests, respectively.

Clutch size was significantly larger for the specialist RSO than for the generalist JSO (Mean \pm SD: 2.76 \pm 0.56 for RSO and 2.29 \pm 0.5 for JSO; Mann-Whitney-Wilcoxon test : $U = 1968$, $P < 0.001$; Fig. 2a), but there was no significant difference in the number of fledglings (Mean \pm SD: 1.92 \pm 1.23 for RSO and 1.88 \pm 0.67 for JSO; Mann-Whitney-Wilcoxon test : $U = 3265$, $P = 0.22$; Fig. 2b). This was because nesting failure was 6.8 times higher for RSO than for JSO: RSO failed to produce fledglings in 37 nests (26.2%), whereas JSO failed in only 2 nests (3.8%) (Fisher's exact probability test: $P = 0.0004$).

Of the two unsuccessful nests of the generalist, JSO, one was predated by an

unknown predator and the other was abandoned, probably due to human disturbance. Of the 37 unsuccessful nests of the specialist, RSO, 21 (56.7%) were predated, 11 (29.7%) were unhatched, and five (13.5%) failed for other reasons (Table 1). Of the 21 predated nests, 17 (81.0%) were predated by the Ryukyu odd-tooth snake. In all 17 direct observations, the Ryukyu odd-tooth snake consumed all the eggs or nestlings. This may characterize the snake's predation pattern and indicates that the snake swallows the whole body or egg. Of the four cases of predation by unknown predators, eggs or nestlings were fully consumed in three cases and partly consumed in one case, suggesting that the former predation was by the Ryukyu Odd-tooth Snake. Importantly, the predation risk of RSO was 7.5 times higher than that of JSO (predated nests: RSO = 21, JSO = 1; not predated nests which bred successfully or failed for other reasons: RSO = 129, JSO = 52, Fisher's exact probability test $P < 0.0001$) and the predation was concentrated on the eggs or early hatching stages of the specialist RSO (Fig. 4).

Snake activity

During the night road census, we observed a total of 25 snakes, of which 22 (88%) were the main predator, Ryuku Odd-tooth Snake (two for Okinawa Habu and one for Ryukyu Green Snake). Here, we show the results including all the snakes, but the results were essentially the same when using only data on Ryuku Odd-tooth Snake. No snake was observed at temperatures below 16°C (Fig.3). The number of snakes observed increased with increasing temperature (GLM: $Z= 2.0$, $P= 0.045$; Fig. 3). Based on the regression and the daily minimum temperature monitored by the Meteorological Bureau of Japan, we estimated the relative activity of snakes during the breeding seasons of scops owls (Fig. 4). The estimated snake activity was at low levels until late

April, increased from early May, and approached its peak in June.

Discussion

Breeding timing, especially the nesting season, of the dietary specialist RSO coincided with the emergence of their main prey item, orthopterans (Toyama and Saitoh 2011), but also with snake activity (Fig. 4). As a result, nest predation of RSO was considerably higher than that of JSO, which bred one month earlier than RSO. Nest site selection could also have significant effects on predation rate (Rosenzweig 1987, Martin 1988, 1998), but difference in breeding timing was more important factor in the present study. Nest boxes set in lower height indeed had a higher predation rate than those in higher height (M. Toyama, N. Kotaka, and I Koizumi. unpublished data). However, even though RSO selected higher nests (M. Toyama, N. Kotaka, and I Koizumi. unpublished data), predation rate was significantly higher in JSO than RSO. Therefore, the difference in predation rate between the species was mainly due to the difference in breeding timing. Although our comparative approach cannot be a proof, the clear results may infer that a trade-off exists between food availability and nest predation risk and both could influence the timing of breeding.

Several factors could explain the difference of breeding timing between the syntopic scops owls other than predation avoidance. First, JSO may innately have an earlier breeding season than RSO (i.e., a phylogenetic constraint). Although only fragmented data are available, the timing of JSO fledging varies widely from late May to early July on Honshu Island, Japan (Kobayashi et al. 1999; Ito and Akasaka 2004), overlapping with the fledging timing of RSO on Okinawa Island. In fact, Okinawa

Island is the southern limit of their distribution and considered as earliest breeding area in this species. Therefore, JSO may have the potential to breed much later, in the same season as RSO, on Okinawa Island.

Second, JSO might have adjusted earlier breeding timing to coincide with a greater abundance of prey items whose abundance reaches a peak during mid–April to late–May (i.e., the JSO nesting season). If this is the case, the diet of JSO should be biased toward the abundant prey(s). JSO, however, consumed a variety of prey items during the nesting season, including orthopterans (Toyama and Saitoh 2011). Furthermore, the diet composition of JSO changed throughout the breeding season (Toyama and Saitoh 2011), indicating that they forage accessible prey depending on the abundance of each prey. Therefore, it seems that JSO did not strongly adjust its breeding timing for particular prey species.

Third, JSO may have brought its breeding season forward due to nest competition with RSO. Coexisting species may temporally partition limited resources, such as tree cavities (Ingold 1994; 1996; Wiebe 2003). However, for JSO to take priority over RSO, only a slight shift in breeding season would be sufficient; a one-month difference is not necessary. In addition, considering larger body size in JSO, JSO may outcompete RSO. Rather, the earlier breeding seems more likely to be a response to snakes. Figure 4 can be interpreted as the JSO nestlings growing large enough to escape from snake predation, resulting in a very low predation rate (1.9%).

If the dietary generalist JSO shifted its breeding timing to avoid nest predation, some costs might have been incurred. For example, as discussed above, food resources might not have approached their maxima when the owl bred. Interestingly, clutch size and the number of fledglings of JSO on Okinawa Island (mostly two- with a few

three-fledgling nests) were smaller than those on Honshu Island (up to six fledglings, Kobayashi et al. 1999; Ito and Akasaka 2004). This suggests that JSO on Okinawa may not be able feed their nestlings enough, because they breed in a season with relatively low food resources to avoid nest predation.

Despite the possibility, to demonstrate the effects of nest predation on breeding timing is difficult. We made use of the advantages of the study area, such as comparative species with different niche width, a single reptilian predator, and less intensity of pulse food resources. Our results, however, did not conclusively prove that JSO shifted its breeding season in response to snake predation due to the lack of controlled sites and replications. One of the best approaches to clarify the combined effects of predators and competitors on breeding timing would be to compare different locations where predators and/or competitors are present or absent. Unfortunately, this was not possible in our study site because there was no location with a similar environment where only JSO were present. Another approach may be a field experiment to remove predators to see if breeding timing changes or not. This, however, is extremely difficult and costly. Further research is needed to better understand the roles of predation on reproductive timing.

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Figure legends

Fig. 1. Breeding timing of scops owls in the forest of Okinawa Island during 2006–2008 (data on 2004-2005 were not shown due to low sample size). White bars represent the Japanese Scops Owl ($n = 14$ in 2006, $n = 21$ in 2007, $n = 15$ in 2008) and black bars represent the Ryukyu Scops Owl ($n = 29$ in 2006, $n = 31$ in 2007, $n = 34$ in 2008).

Fig. 2. Clutch size (a) and number of fledglings (b) of the Japanese Scops Owls (white bars, clutch size: $n = 51$, number of fledglings: $n = 52$) and the Ryukyu Scops Owl (black bars, clutch size: $n = 130$, number of fledglings: $n = 141$). Category zero in clutch size is shown for the comparison between the upper and lower panels, and does not mean that a pair laid no eggs.

Fig. 3. Relationship between numbers of Ryukyu Odd-tooth Snakes (snake activity) and temperature. The size of a circle represents the number of surveys. No snakes were observed below 16°C.

Fig. 4. Seasonal changes in predation risk (estimated snake activity), the number of

bush-crickets (main prey of the Ryukyu Scops Owl), and predation events together with breeding timing of the scops owls. The bold line indicates estimated snake activity calculated from the coefficients of the GLM between snake observation and temperature ($\log(y) = 0.11 x - 2.54$ where y is snake count and x is daily minimum temperature). The dashed line indicates the relative abundance of bush-crickets estimated based on singing events (modified from Toyama and Saitoh 2011). Black triangles and squares indicate nest predation of Ryukyu Scops Owls by snakes and unknown predators, respectively.

Table

Table 1. Breeding success and causes of nesting failure in Japanese and Ryukyu Scops

Owls. Numbers of events and percentages (in parentheses) are shown.

	Japanese Scops Owl	Ryukyu Scops Owl
	<i>n</i> (%)	
Success	51(96.2)	113(76.9)
Predation	1 (1.8)	21 (13.9)
No egg hatched	1 (1.8)	11 (7.3)
Failure for Other reason	0	5 (5.3)
Total	53 (100)	150 (100)