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Author(s)	Murakami, Ryota; Sawada, Akira; Ono, Haruka; Takagi, Masaoki
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ORIGINAL ARTICLE

The effect of experience on parental role division in Ryukyu Scops Owl *Otus elegans*

Ryota MURAKAMI*, Akira SAWADA, Haruka ONO and Masaoki TAKAGI#

Department of Natural History Science, Graduate School of Science, Hokkaido University, Kita 10, Nishi 8, Kita-ku, Sapporo 060–0810, Japan

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Abstract Parental role division is common among monogamous birds. Among raptors, males typically expend more effort to feed their chicks than do females, yet few studies have focused on how each pair establishes this role division. Therefore, in this study we examined the mechanism of role division in the Ryukyu Scops Owls *Otus elegans* on Minami-daito Island. Pairs of this species typically remain together and use the same nest over several years, so there is a possibility that their role division improves with experience over time. To clarify this, we studied the feeding frequency and territorial usage of individuals. Males fed their chicks more frequently than females, and experienced individuals using the same nests fed their chicks more than inexperienced individuals. On comparing experienced and inexperienced pairs, we found that experienced individuals hunted closer to the nest than inexperienced individuals. Furthermore, the home ranges of the males and females of experienced pairs, overlapped less than those of inexperienced pairs. Experience of using a nest site in consecutive years may allow such individual behavioural differences to develop and be involved in role division in parental care.

Key words Experience, Feeding, *Otus elegans*, Territorial usage

Sexual differences in avian foraging behaviour during the breeding season are widely recognised. Among raptors, males and females typically share in brood-rearing (Royle et al. 2006; Kontiainen et al. 2009; Evans & Stutchbury 2012). Males are often responsible for feeding, while females are responsible for incubating their eggs, and brooding their chicks (Newton 1978; Collopy 1984; Holthuijzen 1990; Margalida et al. 2010; Martinez et al. 2020). To meet the tremendous demands from chicks, males make efforts to maximize their foraging volume. Therefore, the amount of food required differs between males and females during this season; males need to capture more food than do females. However, it is not clear how pairs establish this division.

Foraging patterns also vary depending on factors other than sex. In birds, experience influences foraging behaviour (Forslund & Pärt 1995). Older individuals, having experienced more interactions with

various environmental factors, exhibit more optimal patch selection (Franks & Thorogood 2018). Their accumulated experience may allow them to appropriately evaluate the surrounding environment and select patches with higher gains (Mery & Burns 2010; Whitfield et al. 2014; Franks & Thorogood 2018). Not only personal experience, but also one's mate's experience may be important. This experience may lead to the establishment of a more efficient sharing of feeding duties. Experienced males should be more efficient foragers and feeders than inexperienced ones. Even where there are differences in factors such as territorial environment, experience may affect many owl individuals in the same way. To clarify the value of experience, and to understand the influence of sex, it is necessary to examine foraging-behaviour differences during the breeding season. Because the effects of sex and experience on breeding behaviour are obvious in long-lived species with sexual size dimorphism and lifelong monogamy, such as seabirds and raptors, they make good study species for this subject.

To verify the interaction between experience and

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Corresponding author, E-mail: mtakagi@eis.hokudai.ac.jp

* Present address: Atmosphere and Ocean Research Institute, The University of Tokyo, Kashiwa, Chiba 277–8564, Japan

sex and their effects on feeding behaviour, we used the population of Ryukyu Scops Owls *Otus elegans* on Minami-daito Island. These monogamous owls rarely change their territories or partners (Nagai et al. 2018; Takagi 2020). As in other owl species, the Ryukyu Scops Owl exhibits reversed sexual dimorphism – females are larger than males (Akatani 2011; Sawada et al. 2020). The experience of nest usage differs among pairs because of differences in the year of birth and first breeding. Past research has revealed that there are individual differences in the types of food delivered to chicks (Takagi & Akatani 2011). These differences might have been due to differences in experience of their nest usage. They may have improved their foraging efficiency and breeding behaviour over time by adapting to the environment around their nest.

Minami-daito Island is a small island (22 km in circumference and 32 km² in area), located about 400 km east of the main island of Okinawa. The owls live at a very density in the forests of this island (Takagi et al. 2007a; Sawada et al. 2018). Being a small isolated oceanic island, the diversity of insects available as prey for owls is predictably low (MacArthur & Wilson 1963). Nevertheless, Ryukyu Scops Owls exhibit individual differences in the prey types they hunt (Takagi & Akatani 2011). This suggests that they are selective, for some reason, despite the limited range of prey available. Sexual or experiential differences may affect individual differences in foraging, prey and food quantity.

In this study, we aimed to examine and discuss the influence of experience on the feeding behaviour of male and female Ryukyu Scops Owls. To this aim, we investigated and compared home ranges and prey taken, in relation to individual differences in factors such as sex and breeding experience. Finally, we discuss the influence of experience on reproductive and foraging strategies in each sex, based on these differences.

MATERIALS AND METHODS

1) Study site and material

Ryukyu Scops Owls on Minami-daito Island uses nest cavities in introduced casuarina *Casuarina spp.*, native Fountain Palm *Livistona chinensis var. amanoi*, or nest boxes (Akatani et al. 2011). Nesting habitat for this species is concentrated in thin bands of woodland, which they habit very densely (Takagi et al. 2007a; Takagi et al. 2007b; Sawada et al. 2018).

A single clutch consists of one to four eggs (Takagi et al. 2007b; Sawada A & Iwasaki T unpublished data).

2) Feeding Record

We recorded the feeding behaviour of 25 pairs using nest boxes in 2019. When the first chick was between 15 and 20 days old, we recorded feeding behaviour for two hours (from 1900 to 2100) using CCD cameras (custom-made CCD cameras; Wireless Tsukamoto, Suzuka-shi, Japan) attached to the nest box entrances or placed insides. This time scale follows that of Takagi and Akatani (2011). Some recording days were shifted by up to three days due to extremely bad weather preventing deployment of recording equipment. For each feeding event, we recorded the prey items, the sex of the feeding individual, and the time (the time of return to the nest and the time of departure from the nest) from the videos. We specified the prey taxa to orders following Takagi and Akatani (2011). We identified the sex of the parents based on their colour rings. We counted the number of feeding events for the analysis as the frequency of feeding per two hours, and used the Shannon-Wiener diversity index to calculate the diversity of prey for individuals (Poonswad et al. 1998).

3) Movement Tracking

To record their foraging trips during foraging behaviour, we attached GPS loggers (Pinpoint-10 or Pinpoint-50; Biotrack Ltd, Wareham, UK) to two pairs of owls and 10 males in 2019. GPS loggers were deployed about two days before recording; Pinpoint-10 loggers record up to 80 points at 1-minute intervals and Pinpoint-50 loggers record more than 80 points. We programmed the loggers to record 80 points in total, at 1-minute intervals for 80 minutes (from 1900 to 2020) on the day of recording feeding. To filter out unreliable data, we eliminated those with an HDOP value of 5.0 or higher following the instructions of the manufacturer. HDOP value is an indicator of accuracy of the coordinates the GPS loggers recorded; coordinates recorded from fewer than three satellites have errors measured in dozens of meters (Marquardt et al. 2017). As the owls' home ranges were smaller than 40,000 m² (equivalent to a 200 m square; see results), we only used coordinate data obtained from more than four satellites as recording points. From this data, we calculated the distances from the recorded points to the nest. Home ranges were determined by kernel density estimation

(50% Kernel area) using the recorded points with “AdehabitatHR” (Calenge 2006), a package for statistical software R version 4.0.1 (R Core Team 2020). The percentage of overlap (PO) in a pair’s home range was calculated as $PO = O/U$, where O is the area of overlap, and U is the total area of the home ranges of the male and female.

4) Data Analysis

We used generalized linear models (GLM) and generalized linear mix models (GLMM) to examine the effects of each factor recorded. Here, we defined the explanatory variables as follows: 1) *Experience of male* (Binary variable: 1=presence, 0=absence), 2) *Experience of female* (Binary variable: 1=presence, 0=absence), 3) *Experience of each individual* (Binary variable: 1=presence, 0=absence), 4) *Age of chicks* (Continuous variable), 5) *Sex* (Binary variable: 1=male, 0=female), 6) *Number of chicks* (Continuous variable), 7) *Individual body mass*, 8) *Food categories* (Categorical variable: 1=araneae, 2=blattodea, 3=Scolopendromorpha, 4=orthoptera, 5=squamata), 9) *The frequency of appearance of each prey category*. Because we were unable to specify the breeding experience of some individuals, the parameters of *Experience of male*, *female*, and *individual experience* were defined as the experience of nest usage instead of breeding. The years of experience ranged from zero to eight for each individual. The indexes of experience were binarized for simplification. *Experience of each individual* was used only in the analysis using the data of two pairs because one of these pairs was experienced (experienced male and female) and one was inexperienced (inexperienced male and female). All GLM and GLMM analyses were conducted using the “glm” or “glmer” functions in the R package “lme4” (Bates et al. 2015). The most parsimonious model was selected on the basis of the Akaike information criterion (AIC) using “step” function in the R package “MuMIn” (Bartoń 2020). We evaluated the effect of each explanatory variable by Wald test on the regression coefficients of the best model. The explanatory variables were standardized before the analyses. In cases using categorical data, such as sex, a dummy variable was set for each category and standardized. The estimate values are expressed as mean±S.E.

Feeding Contents

To examine individual differences in feeding, we performed the Friedman test for the prey items of

individuals.

To investigate whether differences in foraging strategies arise from sex or experience affecting prey content diversity, GLMM was conducted for prey diversity with three explanatory variables: *Experience of male*, *Experience of female*, and *Sex*. Nest ID was used as a random effect. The error structure had a Gamma distribution, and the link function was *inverse* in this model.

To investigate the factors affecting feeding frequency, we also conducted GLMM with four explanatory variables: *Experience of male*, *Experience of female*, *Age of chicks*, and *Sex*. We used nest ID as a random effect and the number of chicks in each nest as the offset term. The error structure had a Poisson distribution, and the link function was *log* in this model.

Time spent in the nest at feeding varied among individuals. Therefore, GLMM was conducted for length of stay (time in seconds while in the nest) with five explanatory variables: *Experience of male*, *Experience of female*, *Age of chicks*, *Sex*, and the interaction between *Sex* and *Age of chicks*. Nest ID was used as a random effect. The error structure had a Poisson distribution, and the link function was *log* in this model. If they did not enter the nest and handed over prey at the entrance, the length of stay was considered to be zero seconds.

Foraging Behaviour

To examine differences in foraging behaviour by experience and sex, we conducted GLM for distances from each recording point to the nest for individuals, using the data of two pairs with three explanatory variables: *Experience of each individual*, *Age of chicks*, and *Sex*. The error structure had a Gamma distribution, and the link function was *inverse* in this model.

Regression analysis by GLMM was conducted for distance from the nest of males with five explanatory variables: *Experience of male*, *Age of chicks*, *Number of chicks*, *Individual body mass*, and the interaction between *Experience of male* and *Age of chicks*. Nest ID was used as a random effect. The error structure had a Gamma distribution, and the link function was *inverse* in this model.

We estimated the length of foraging trips by comparing the feeding data obtained during the same period with the GPS coordinates and used the sum of the direct distances between each successive point from the time they left the nest to the time they

returned as the distance of the foraging trip. Only those foraging trips with records of both leaving and returning were calculated, using the data with both feeding data and GPS data. The above calculations allowed us to record foraging trips for six categories of prey in this study. Distance data were categorized by prey content for each trip. Regression analysis by GLMM was conducted for the length of foraging trips with three explanatory variables: *Food categories*, *The frequency of appearance of each category*, and *The number of chicks*. Nest ID was a random effect. The error structure had a Gamma distribution, and the link function was *inverse* in this model.

RESULTS

1) Feeding

As with a previous study by Takagi and Akatani (2011), individual differences in feeding frequency were confirmed in this research (Friedman test, chi-squared=70.49, $P<0.05$). Most individuals mainly carried terrestrial animals (Table 1); blattodea and araneae were the first and second most frequent prey items regardless of the experience of males or females. The two orders accounted for more than 50% of the total prey contents for 38 out of 50 individuals. The next most frequent prey was Orthoptera; it was particularly common in nests where blattodea and araneae were less frequent. Four pairs had one experienced member, 13 pairs had both an experienced male and an experienced female, and eight pairs had an inexperienced male and an inexperienced female. The differences in prey diversity among individuals were not explained by sex, experience, or chick age (Table 2).

We adopted the model of feeding frequency, without the offset term based on AIC (Table 2). In this model, there were significant effects on feeding frequency of experience of males (Estimate=0.233±0.082; Wald test, $Z=2.83$, $P<0.05$) and sex (Estimate=0.148±0.035; Wald test, $Z=4.22$, $P<0.05$) (Table 3). From these estimates, males tended to feed 1.15 times more frequently than females, and pairs with experienced males fed 1.26 times more frequently than pairs with inexperienced males. The age of the chicks did not affect feeding frequency by either sex.

For the time spent in the nest, we adopted the model with sex, chick age, and their interactions as explanatory variables (Table 2). A significant effect was found for chick age (Estimate=-0.488±0.008; Wald test,

Table 1. Food contents

Male Experience	Female Experience	Sex	Number of Nest	Araneae	Blattodea	Scolopendromorpha	Lepidoptera	Odonata	Orthoptera	Squamata	Total	Others
Experienced	Experienced	Female	13	54 (27.1)	71 (35.6)	11 (5.5)	14 (7.0)	2 (1.0)	12 (6.0)	21 (10.6)	199 (100.0)	14 (7.0)
		Male	13	76 (31.4)	82 (33.9)	6 (2.5)	10 (4.1)	2 (0.8)	27 (11.2)	23 (9.5)	242 (100.0)	16 (6.6)
Experienced	Inexperienced	Female	2	4 (12.9)	15 (48.4)	4 (12.9)	—	—	3 (9.7)	3 (9.7)	31 (100.0)	2 (7.6)
		Male	2	9 (17.0)	15 (28.3)	6 (11.3)	7 (13.2)	1 (1.9)	9 (17.0)	5 (9.4)	53 (100.0)	1 (1.9)
Inexperienced	Experienced	Female	2	5 (45.5)	2 (18.2)	—	—	—	1 (9.1)	2 (18.2)	11 (100.0)	1 (9.1)
		Male	2	11 (42.3)	8 (30.8)	1 (3.8)	—	—	—	2 (7.7)	26 (100.0)	4 (15.4)
Inexperienced	Inexperienced	Female	8	23 (23.2)	35 (35.4)	5 (5.1)	1 (1.0)	4 (4.0)	13 (13.1)	13 (13.1)	99 (100.0)	5 (5.0)
		Male	8	54 (36.2)	36 (26.2)	5 (3.4)	—	—	30 (20.1)	15 (10.1)	149 (100.0)	9 (6.0)

Numbers in parentheses are percentages of each food category (rounded to two decimal places). All groups were dominated by Araneae and blattodea, followed by orthoptera and squamata.

The effect of experience on feeding

Table 2. AIC values for each model ($\Delta AIC \leq 2.0$)

Response value	Model	AIC	ΔAIC
Food Diversity	~ 1	66.3	0
	$\sim \text{Experience of male}$	66.7	0.4
	$\sim \text{Experience of female} + \text{Experience of male}$	67.6	1.3
	$\sim \text{Sex}$	67.6	1.3
	$\sim \text{Experience of male} + \text{Sex}$	68	1.7
	$\sim \text{Experience of female}$	68.3	2
Feeding Frequency	$\sim \text{Chick age} + \text{Experience of female} + \text{Experience of male} + \text{Sex}$	562.9	0
	$\sim \text{Chick age} + \text{Sex} + \text{Offset}(\log(\text{The number of their chicks}))$	563.1	0.3
	$\sim \text{Chick age} + \text{Experience of female} + \text{Sex} + \text{Offset}(\log(\text{The number of their chicks}))$	563.5	0.7
	$\sim \text{Experience of female} + \text{Experience of male} + \text{Sex}$	563.9	1.1
	$\sim \text{Chick age} + \text{Experience of male} + \text{Sex}$	564.2	1.3
	$\sim \text{Chick age} + \text{Experience of male} + \text{Sex} + \text{Offset}(\log(\text{The number of their chicks}))$	564.8	1.9
Nest staying time	$\sim \text{Chick age} + \text{Sex} + \text{Chick age} * \text{Sex}$	66775.2	0
	$\sim \text{Chick age} + \text{Experience of male} + \text{Sex} + \text{Chick age} * \text{Sex}$	66776.7	1.6
	$\sim \text{Brood Size} + \text{Chick age} + \text{Sex} + \text{Chick age} * \text{Sex}$	66776.8	1.6
	$\sim \text{Chick age} + \text{Experience of female} + \text{Sex} + \text{Chick age} * \text{Sex}$	66777.1	1.9
Distance from nest(pair)	$\sim \text{Experience of each individual} + \text{Sex}$	5354.8	0
	$\sim \text{Chick age} + \text{Experience of each individual} + \text{Sex}$	5355.5	0.8
Distance from nest (male)	$\sim \text{Chick age} + \text{Experience of male} + \text{Chick age} * \text{Experience}$	25177.1	0
	$\sim \text{Chick age}$	25178.2	1.1
	$\sim \text{Chick age} + \text{Experience of male}$	25178.4	1.3
	$\sim \text{Chick age} + \text{Experience of male} + \text{The number of their chicks} + \text{Chick age} * \text{Experience}$	25179.1	1.9
	$\sim \text{Body mass of the tagged individual} + \text{Chick age} + \text{Experience of male} + \text{Chick age} * \text{Experience of male}$	25179.1	2
Foraging trip	$\sim \text{The number of their chicks}$	467.2	0
	~ 1	467.6	0.4

Table 3. Estimates of GLMM for feeding frequency

Explanatory variables	Estimate	Std. Error	z value	P
<i>Chick age of chicks</i>	-0.0625	0.0357	-1.75	0.08
<i>Experience of female</i>	-0.1529	0.0814	-1.88	0.06
<i>Experience of male</i>	0.2328	0.0821	2.84	0.005
<i>Sex</i>	0.1478	0.035	4.22	<0.001

The estimates of female and male experiences represent the effect of the experienced individuals compared to the inexperienced, and sex represents the effect of males compared to females. Standardized data were used for all explanatory variables.

$Z = -56.67$, $P < 0.05$), sex (Estimate = -0.233 ± 0.007 ; Wald test, $Z = -16.58$, $P < 0.05$), and their interaction (Estimate = 0.078 ± 0.007 ; Wald test, $Z = 10.51$, $P < 0.05$) (Table 4). Time spent in the nest decreased by 2.80 s per day as the chicks aged. Females tended to stay 1.60 times longer than males. Interactions indicated that the reduction in time spent in the nest was greater for females than for males.

Table 4. Estimates of GLMM for time spent at the nest

Explanatory variables	Estimate	Std. Error	z value	P
<i>Chick age</i>	-0.4884	0.0078	-62.7	<0.001
<i>Sex</i>	-0.2333	0.0074	-31.44	<0.001
<i>Chick age * Sex</i>	0.078	0.0074	10.51	<0.001

Sex indicates the effect of males compared with females. Both explanatory variables use standardized data.

2) Foraging

The home range overlap for males and females was smaller for experienced pairs than for inexperienced pairs (Fig. 1, Table 5). Home range sizes were 34,657 m² for males and 37,611 m² for females of inexperienced pairs (Fig. 1a), and 7,039 m² for males and 10,837 m² for females of experienced pairs (Fig. 1b). The overlap in the home ranges of mates in experienced pairs was 5.4% and 49.2% for inexperienced pairs. In experienced pairs, males tended to forage close to the nest, whereas female foraged further from the nest. In contrast, inexperienced males

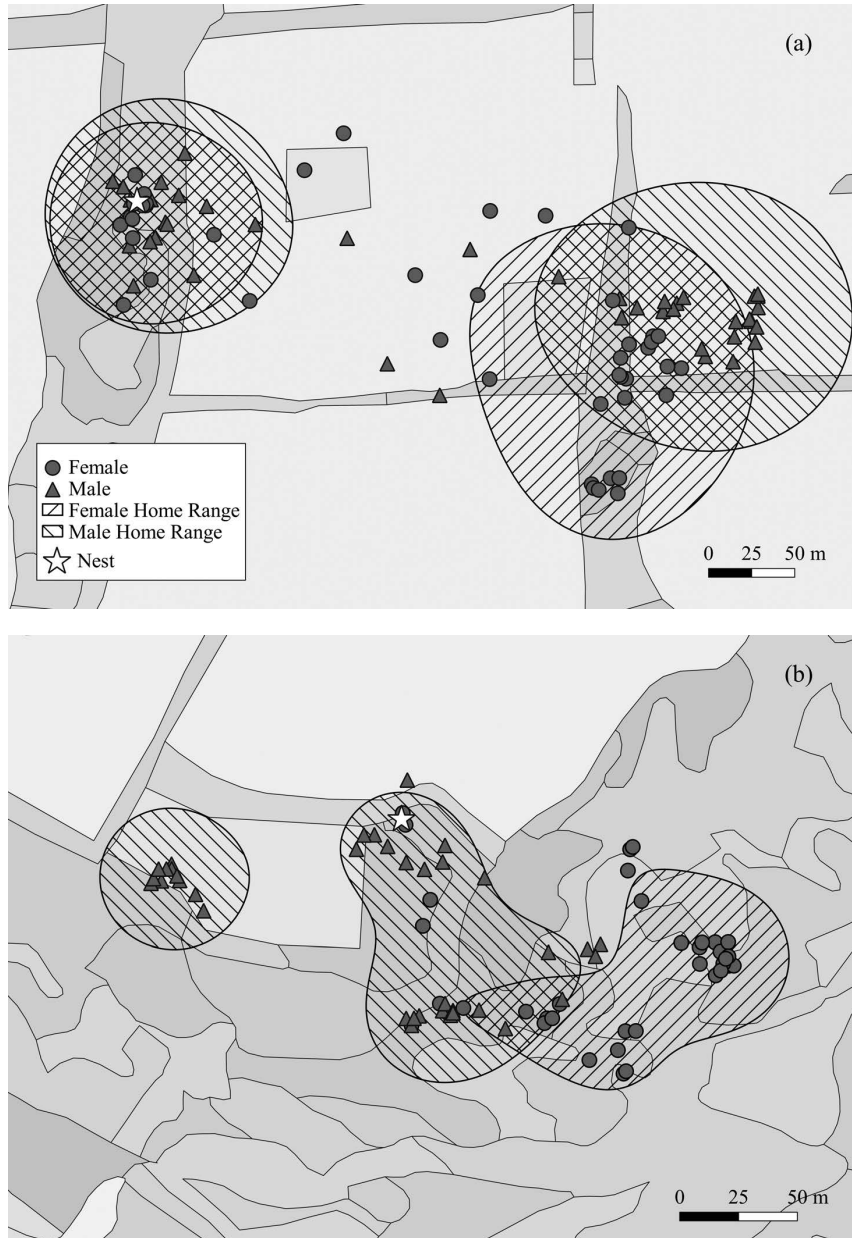


Fig. 1. Home ranges of the inexperienced (a) and the experienced pair (b).

Figures were generated by QGIS 3.10.7 (QGIS Development Team 2020). Home ranges were defined by the kernel core (inside the 50% kernel contour).

and females used their territories in the same way. In the model for the area used by pairs (distance from recorded point to nest), the model using sex and experience as explanatory variables had the lowest AIC values (Table 2). Both effects were significant, with females tending to use 1.19 times farther places than males (Estimate=0.001±0.001; Wald test, $t=2.81$, $P<0.05$) and inexperienced individuals tending to use 1.74 times farther places (Estimate=0.005±0.001;

Table 5. Home range sizes of experienced and inexperienced pairs

	Experienced	Inexperienced
Number of female plots	58	55
Number of male plots	71	63
Female home range (m ²)	10,837	37,611
Male home range (m ²)	7,039	34,657
Overlap area (%)	5.4	49.2

Table 6. Estimates of GLM for distances from the nest to recording points of two pairs

Explanatory variables	Estimate	Std. Error	t value	P
<i>Sex</i>	0.0007	0.0003	2.81	0.005
<i>Experience of male</i>	0.0023	0.0003	7.73	<0.001

Sex represents the effect of males compared with females, and experience represents the effect of experienced compared with inexperienced individuals. Standardized data were used for both explanatory variables.

Table 7. Estimates of GLMM for distances from the nest to the recording points of males

Explanatory variables	Estimate	Std. Error	t value	P
<i>Experience of male</i>	0.0019	0.0014	1.4	0.161
<i>Chick age</i>	-0.0006	0.0002	-2.55	0.011
<i>Experience* Chick age</i>	0.0004	0.0002	1.82	0.069

Male experience indicates the effect of inexperienced individuals compared with experienced. Standardized data were used for both explanatory variables.

Wald test, $t=7.73$, $P<0.05$) than experienced ones (Table 6).

In the model for the area used by males (distance from the recorded point to the nest), the model using chick age, experience, and their interaction as explanatory variables had the lowest AIC values (Table 2). Although there was no significant effect on the distance to the point of use by experience, there was a significant change (Estimate= -0.001 ± 0.000 ; Wald test, $t=2.55$, $P<0.05$) with which age (Table 7), and they tended to use areas 1.02 m farther away from their nests each day.

In the model of foraging trip length, the model using the number of chicks as an explanatory variable had the lowest AIC value (Table 2). However, the effect of the number of chicks was not significant (Estimate= -0.001 ± 0.001 ; Wald test, $t=-1.63$, $P=0.102$).

DISCUSSION

1) Feeding behaviour

Low food diversity is a biogeographical characteristic of remote, oceanic islands, and in this Minami-daito Island is typical. This low diversity may explain the absence of significant differences in the diversity of feeding contents between any groups

of Ryukyu Scops Owls. Remote oceanic islands, such as Minami-daito Island, have lower rates of immigration and higher rates of population extinction (MacArthur & Wilson 1963). Thus, the diversity of animal species available for the owls is expected to be small. Although our results confirmed that there were individual differences in prey items taken, we were unable to confirm that the food diversity brought to the chicks varied with differences in foraging strategies in relation to either sex, experience, chick age. Because the home ranges of owls in this study were just a few hundred meters square, the type of vegetation growing within each territory may bias the availability of prey species within each territory. Since high-quality prey are not always available in sufficient quantities in their territories, the owls may preferentially feed on species that are encountered frequently in patches within their territories, in other words their prey selection is essentially impulsive (Matsushima & Aoki 2005). In order to clarify territory usage and selection of prey, we must confirm differences in vegetation distribution and food quality.

2) Sexual difference

In Ryukyu Scops Owls, sexual differences in the cost of breeding may be responsible for the differences we found between males and females in the amount of food they invested in their chicks. Female birds in general have higher costs of reproduction (egg laying and incubation) than do males (Bradley et al. 2002; Klimczuk et al. 2015; Zuberogitia et al. 2018). Male raptors often compensate for this cost asymmetry by being the main food providers for their chicks (Newton 1978; Collopy 1984; Holthuijzen 1990; Margalida et al. 2010; Byholm et al. 2011). In this study of Ryukyu Scops Owls, males provided food more frequently than did females. However, females remained longer in the nest after feeding than did males. Males might feed not only their chicks but also their partners in the nest during that time. Thus, in this species, males may feed their chicks and partners frequently to compensate for their mate's investment in egg-laying.

Males may frequently forage close to the nest to maximize the amount and efficiency of their investment in their chicks. In some species, females regulate their feeding efforts based on those of their partners (Johnstone & Hinde 2006; Wieringa et al. 2019). Location data showed that males hunted closer to the nest than females. Males may need to obtain more

food to feed their chicks and females as well. Thus, males may more actively use the area around their nest to meet their food requirements.

3) Experience

Experience may be involved in the mechanism of efficiently sharing feeding duties between pair members. The number of pairs of which both males and females were experienced was more than the number of pairs in which only one of the mates was experienced. The annually accruing experience of each pair member may be one of the advantages of a monogamous breeding system that continues over several years. Our results showed that the effects of experience on feeding frequency, distance from the nest, and home range size depended on whether the pair had used the same nest before or not. These effects were same for both sexes. If their experience leads to a greater understanding of foraging sites within a territory, it seems conceivable that both members of the pair might use the same foraging areas where food is abundant. However, males and females with experience used sites closer to the nest than those without experience, and the overlap in the home ranges of experienced pair members was smaller than that of inexperienced pair members. Only the experience of males significantly affects their feeding frequencies, suggesting that a male's experience may affect this division of roles. Thus, males may actively use areas close to the nest and where food is plentiful, unlike females who invest less feeding effort because males are responsible for most of the feeding. Because we were able only to use two pairs in the analysis of home range size, we cannot declare that the separation of foraging site did not result from the avoidance of individual competition or individual difference, but from parental role division. To clarify this, we need to track other pairs and compare their home range sizes.

There may be both negative and positive reasons for inexperienced individuals to use larger areas than experienced ones. One reason for their high feeding frequency may be that experienced males are able to make more frequent trips between their nest and foraging sites because they use closer locations than inexperienced ones. Individuals judged to have been inexperienced were using their territories for the first time and may not have had time to develop an understanding of the distribution of food resources compared with those individuals with previous experience. This lack of experience perhaps reduces the

probability of them finding suitable foraging sites close to their nests thereby requiring them to travel farther than experienced individuals in order to find food. The increased distance to foraging sites may also reduce feeding frequency at the nest as both mates search away from the nest. We have mentioned the negative factors so far, but there may be a positive factor too when inexperienced individuals use their territories widely – they may gain by gathering information from more habitats. Under experimental conditions in captivity, the Great Tit *Parus major* has been shown to risk using failed foraging sites to assess their profitability (Partridge 1976). Furthermore, Franks and Thorogood (2018) considered that experience contributes to effective evaluation of surroundings and the selection of higher gain patches. Inexperienced individuals, even among Ryukyu Scops Owls in natural environments, may explore larger areas than experienced individuals and thereby identify more profitable foraging sites, and so gain experience.

Experienced males may be able to maintain a high feeding frequency while reducing their cost for breeding. As discussed above, sexual differences in feeding chicks are often due to differences in reproductive costs between males and females. As for the females, mating with experienced males allows them to reduce the costs they incur themselves in a single breeding session because their partner provides more food for their chicks. Such a mating pattern also allows for breeding in such a way that benefits both males and females, as males can efficiently feed chicks and females can strive to minimize their investment in breeding at one time. The advantage of the same partners using the same location repeatedly may make it easier to maintain partners and territories in the Ryukyu Scops Owl.

4) Conclusion and future direction

Ryukyu Scops Owls divide their foraging area between males and females based on reproductive strategies and sexual differences, with males foraging close to the nest and females foraging further away from the nest to achieve the ideal amount of food they need. In long-lived monogamous species, such sharing may be acquired by males continuing to use the same nest and understanding the distribution of food resources within their territory and actively using feeding sites closer to their nest. So, we hypothesise that parents usage of their territories, and the division of their parental roles, becomes

increasingly sophisticated based on their experience.

This hypothesis has been proposed based on descriptive considerations and data from a single year with a small number of samples. There are several issues that we must clarify to verify this hypothesis, such as changes in reproductive performance, overall trends in the relationships between home range size and experience, and the quality of various prey species.

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REFERENCES

- Akatani K (2011) Ryukyu Scops Owl Ryukyu-konohazuku (Jpn) *Otus elegans*. Bird Res News 8: 4–5.
- Akatani K, Matsuo T & Takagi M (2011) Breeding ecology and habitat use of the Daito Scops Owl (*Otus elegans interpositus*) on an oceanic island. J Raptor Res 45: 315–323.
- Bartoń K (2020) MuMIn: Multi-Model Inference. R package version 1.43.17. Available at <https://CRAN.R-project.org/package=MuumIn> (accessed on 19 August 2020).
- Bates D, Mächler M, Bolker B & Walker S (2015). Fitting linear mixed-effects models using lme4. J Stat Softw 67: 1–48.
- Bradley RW, McFarlane LA, Vanderkist BA & Cooke F (2002) Sex differences in nest visitation by chick-rearing Marbled Murrelets. Condor 104: 178–183.
- Byholm P, Rousi H & Sole I (2011) Parental care in nestling hawks: breeding experience and food availability influence the outcome. Behav Ecol 22: 609–615.
- Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model 197: 516–519.
- Collopy MW (1984) Parental care and feeding ecology of Golden Eagle nestlings. Auk 101: 753–760.
- Evans ML & Stutchbury BJM (2012) Nest attendance and reproductive success in the Wood Thrush. Condor 114: 401–406.
- Forslund P & Pärt T (1995) Age and reproduction in birds – hypotheses and tests. Trends Ecol Evol 10: 374–378.
- Franks VR & Thorogood R (2018) Older and wiser? Age differences in foraging and learning by an endangered passerine. Behav Process 148: 1–9.
- Holthuijzen AM (1990) Prey delivery, caching, and retrieval rates in nestling Prairie Falcons. Condor 92: 475–484.
- Johnstone RA & Hinde CA (2006) Negotiation over offspring care – how should parents respond to each other's efforts? Behav Ecol 17: 818–827.
- Klimczuk E, Halupka L, Czyż B, Borowiec M, Nowakowski JJ & Szwiertnia H (2015) Factors driving variation in biparental incubation behaviour in the Reed Warbler *Acrocephalus scirpaceus*. Ardea 103: 51–59.
- Kontinen P, Pietiäinen H, Huttunen K, Karell P, Kolonen H & Brommer JE (2009) Aggressive Ural Owl mothers recruit more offspring. Behav Ecol 20: 789–796.
- MacArthur RH & Wilson EO (1963) An equilibrium theory of insular zoogeography. Evolution 17: 373–387.
- Margalida A, González LM, Sánchez R, Oria J & Prada L (2010) Parental behaviour of Spanish Imperial Eagles *Aquila adalberti*: sexual differences in a moderately dimorphic raptor. Bird Study 54: 112–119.
- Marquardt DD, Scroggs L, Pierce BL, Skow KL, Mote KD & Collier BA (2017) Assessment of GPS transmitters for use on Northern Bobwhite Quail. JSAFWA 4: 100–108.
- Martinez JE, Zuberogitia I, Escarabajal JM, Cerezo E, Calvo JF & Margalida A (2020) Breeding behaviour and time-activity budgets of Bonelli's Eagles *Aquila fasciata*: marked sexual differences in parental activities. Bird Study 67: 35–44.
- Matsushima T & Aoki N (2005) Chick economics: choice based on foraging efficiency. Cognitive Studies 12: 137–141.
- Mery F & Burns JG (2010) Behavioural plasticity: an interaction between evolution and experience. Evol Ecol 24: 571–583.
- Nagai S, Sawada A, Sawada J & Takagi M (2018) Monitoring of fledgling success and improvements of ventilation of FRP nest boxes in Ryukyu Scops Owls from Minami-daito island. The 27th Report of Pro-Natura Foundation: 119–126 (in Japanese with English summary).
- Newton I (1978) Feeding and development of Sparrow-

- hawk *Accipiter nisus* nestlings. *J Zool* 184: 465–487.
- Partridge L (1976) Individual differences in feeding efficiencies and feeding preferences of captive Great Tits. *Anim Behav* 24: 230–240.
- Poonswad P, Tsuji A, Jirawatkavi N & Chimchome V (1998) Some aspects of food and feeding ecology of sympatric hornbill species in Khao Yai National Park, Thailand. In: Poonswad P (ed) *The Asian Hornbills: ecology and conservation*. pp 137–157. White Lotus, Bang Lamung.
- QGIS Development Team (2020) QGIS Geographic Information System. Open Source Geospatial Foundation Project. Available at <https://qgis.org/> (accessed on 19 August 2020).
- R Core Team (2020) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. Available at <http://www.R-project.org/> (accessed on 19 August 2020).
- Royle NJ, Hartley IR & Parker GA (2006) Consequences of biparental care for begging and growth in Zebra Finches *Taeniopygia guttata*. *Amin Behav* 72: 123–130.
- Sawada A, Iwasaki T, Matsuo T, Akatani K & Takagi M (2021) Reversed sexual size dimorphism in the Ryukyu Scops Owl *Otus elegans* on Minami-daito Island. *Ornithol Sci* 20: 15–26.
- Sawada A, Yamasaki T, Iwami Y & Takagi M (2018) Distinctive features of the skull of the Ryukyu Scops Owl from Minami-daito Island, reversed by computed tomography scanning. *Ornithol Sci* 17: 45–54.
- Takagi M (2020) Vocalizations of the Ryukyu Scops Owl *Otus elegans*: individually recognizable and stable. *Bioacoustics* 29: 28–44.
- Takagi M & Akatani K (2011) The diet of Ryukyu Scops Owl *Otus elegans* interpositus owlets on Minami-daito Island. *Ornithol Sci* 10: 151–156.
- Takagi M, Akatani K, Matsui S & Saito A (2007a) Status of the Daito Scops Owl on Minami-daito Island, Japan. *J Raptor Res* 41: 52–56.
- Takagi M, Akatani K, Saito A & Matsui S (2007b) Drastic decline of territorial male Daito Scops Owls on Minami-daito Island in 2006. *Ornithol Sci* 6: 39–42.
- Whitfield M, Köhler A & Nicolson SW (2014) Sunbirds increase foraging success by using color as a cue for nectar quality. *Behav Ecol* 25: 328–334.
- Wieringa A, Klaassen RH, Schlaich AE & Koks BJ (2019) Increased Food Provisioning by Female Montagu's Harriers in Years with Food Shortage Weakens Sex-Specific Roles in Parental Care. *Ardea* 107: 149–158.
- Zuberogoitia I, Martinez JE, Larrea M & Zabala J (2018) Parental investment of male Peregrine Falcons during incubation: influence of experience and weather. *J Ornithol* 159: 275–282.