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FOOD HABITS OF TAWNY FISH-OWLS IN SAKATANG STREAM, TAIWAN

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ABSTRACT.—We examined the diet of Tawny Fish-Owls (*Ketupa flavipes*) living along Sakatang Stream, Taiwan, from January 1994–July 1995 and from February 1998–January 1999. In both number and biomass, aquatic prey constituted the majority of the owls' diet. The most frequently caught prey were small freshwater crabs (*Candidiopotamon spp.*). Nevertheless, the Taiwan mitten crab (*Eriocheir formosa*) and the Taiwan common toad (*Bufo bufo gargarizans*) made up the largest proportion of prey biomass in different years. The breeding activity of prey species appeared to influence their representation in the owls' diet. Large and sluggish prey species such as Taiwan mitten crab and Taiwan common toad were preyed upon more frequently than expected relative to their availability.

KEY WORDS: Tawny Fish-Owl; Ketupa flavipes; diet; Taiwan.

HÁBITOS ALIMENTICIOS DE KETUPA FLAVIPES EN EL ARROYO SAKATANG, TAIWAN

RESUMEN.—Examinamos la dieta de individuos de la especie *Ketupa flavipes* que habitan a lo largo del arroyo Sakatang, Taiwan, entre enero de 1994 y julio de 1995 y entre febrero de 1998 y enero de 1999. Tanto en número como en biomasa, las presas acuáticas constituyeron la mayor parte de la dieta. Las presas capturadas con mayor frecuencia fueron cangrejos pequeños de agua dulce (*Candidiopotamon* spp.). Sin embargo, el cangrejo *Eriocheir formosa* y el sapo *Bufo bufo gargarizans* representaron la mayor proporción de la biomasa de presas en distintos años. La actividad reproductiva de las especies de presas pareció infuenciar su representatividad en la dieta de *K. flavipes*. Las presas de movimiento lento y tamaño grande como *E. formosa* y *B. b. gargarizans* fueron depredadas con una frecuencia mayor a la esperada de acuerdo a su disponibilidad.

[Traducción del equipo editorial]

The Tawny Fish-Owl (*Ketupa flavipes*), a secretive and protected nocturnal raptor, is the largest of the 11 owl species living in Taiwan. This is also the only owl on the island restricted to old-growth riparian forests (Sun et al. 2000). Tawny Fish-Owls eat primarily fish, but also consume small mammals, crabs, reptiles, birds, and insects (Fogden 1973, Meyer de Schauensee 1984, Ali 1986, Voous 1988, Mark et al. 1999) However, these reports were mostly anecdotal or based on limited data. Prior to this study, little was known about the food habits of this owl in Taiwan. The purpose of our study was toexamine the diet of this rare and poorly-known species in the Sakatang Stream of eastern Taiwan.

STUDY AREA AND METHODS

Field work was carried out along Sakatang Stream (24°11′N, 121°35′E) in Taiwan. The 16-km Sakatang Stream study area (100–1300 m elevation) is

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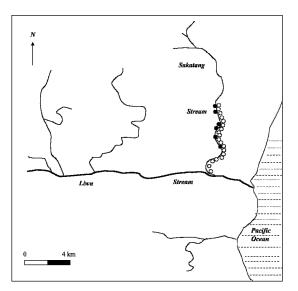


Figure 1. Location of Sakatang Stream study area in eastern Taiwan. Open circles denote stream sections where we searched for owl pellets. Solid circles indicate approximate sites of transect lines established to sample prey abundance.

located 90 km south of Taipei (Fig. 1). The stream runs through a gorge in a mountainous area that rises to 2400 m in elevation (Sun et al. 1997). The mean annual rainfall is 2157 mm. Most precipitation occurs during the summer and early fall typhoon season. The mean annual temperature is 23.3°C. Tropical rainforests, dominated by *Ficus*, Lauraceae, and native ferns, border the lower section of the stream (Hsu 1984).

Each month, from January 1994 to July 1995 and February 1998 to April 1999, we attempted to collect Tawny Fish-Owl pellets along the lower 7-km section of Sakatang Stream. During the study period, we observed at least four owls living along this stream section. Pellets were collected at daytime roosts, under resting/foraging perch sites, and on rocks and logs in the stream. Pellet collection was relatively difficult during the summer and early fall because floods related to typhoons washed away pellets and sometimes made our study site inaccessible. Owl droppings, and occasionally feathers, were frequently found at sites with pellets.

To identify prey species taken by the Tawny Fish-Owl, pellets were brought back to the laboratory and dried with a 60-watt bulb to kill mold. Because most pellets lacked fur or feathers, we easily extracted prey remains without wetting the pellets. Prey remains were identified to the lowest possible

taxa using the identification keys developed by Sun (1996), in which Amphibian species were identified by the shape (e.g., curvature and existence of edge) and length of their limb bones, crustacean prey were identified by their chela (e.g., size and color pattern), fish identification was based on skull fragments, and rodent prey were identified by their hair (e.g., existence of bristle). Shrimp (Palaemonidae), insects, and birds were not identified to species because they were rare or they accounted for only a small proportion of the biomass in the owls' diet. In each pellet, the minimum number of individuals of each prey species was calculated by dividing the total number of chelae, skull components (e.g., preopercula), appendages, or mandibles in the pellet by the number of specific parts possessed by that individual prey type.

To determine the energy contribution of each prey species to Tawny Fish-Owl diets, we trapped and measured selected linear features and mass of prey species from our study site to facilitate the estimation of prey biomass. We measured the depth of crustacean chela, the tibio-fibula length of amphibian legs, and the length of the preoperculum of fish skulls. To calculate the biomass of different prey species, we used regressions for body mass and tibio-fibula length (amphibian) and body mass and length of the preoperculum (fish; Table 1). The body mass of the spinous countryrat (Niviventer coxinga) was obtained from Changchien (1989). The mass of a small passerine bird the size of a Plumbeous Water-Redstart (Rhyacornis fuliginosus) was taken from Cheng (1993).

We also examined the selection of common prey species by Tawny Fish-Owls. Estimates of prey abundance provided an index of food availability and the proportion of the owls' diet that comprised each prey species served as a measure of prey consumption. We identified five types of stream habitat: (1)low-gradient riffle (LR)-current ≤ 0.5 m/sec, with rocks above water surface ≤ 5 m apart; (2) high-gradient riffle (HR)—current >0.5 m/sec, with rocks above water surface ≤ 5 m apart; (3)run (RN)-current >0.5 m/sec, with rocks above water surface, >5 m apart; (4)shallow (SH)—current ≤ 0.5 m/sec, ≤ 30 cm in depth, with rocks above water surface >5 m apart; and (5) pool (PL)—current ≤ 0.5 m/sec, >30 cm in depth, with rocks above water surface >5 m apart). For each stream habitat type, we counted the number of individuals of each potential prey species observed within 3 m on both sides of each transect line within

Species	REGRESSION EQUATION	R VALUE	df	P-VALUE
Taiwan common toad (Bufo bufo gargarizans)	$y = 56.5 \times -90.8$	0.81	26	< 0.001
Brown tree frog (Buergeria robustus)	$y = 23.3 \times -52.0$	0.88	29	< 0.001
Tip-nosed frog (Rana swinhoana)	$y = 19.1 \times -50.2$	0.88	35	< 0.001
Japanese tree frog (Buergeria japonicus	$y = 1.8 \times +0.2$	0.63	10	0.038
Taiwan mitten crab (Eriocheir formosa)	$y = 68.2 \times -49.4$	0.95	70	< 0.001
Small freshwater crabs (Candidiopotamon spp.)	$y = 8.0 \times -0.3$	0.78	19	< 0.001
Small freshwater shrimp	$y = 1.6 \times +3.0$	0.78	11	0.003
Kooye minnow (Varicorhinus barbatulus)	$y = 46.2 \times -41.4$	0.84	24	< 0.001

Table 1. Regression equations used to estimate biomass of different prey species of the Tawny Fish-Owl in Sakatang Stream, Taiwan. We used regressions for body mass and tibio-fibula length for amphibians, body mass and chela depth for crustaceans, and body mass and length of the preoperculum for fish.

3 hr after dark on nights with little (<5 mm) or no rain. The total length of the transect lines, which ran up and down the stream, in each habitat were: LR, 794 m; HR, 491 m; RN, 148 m; SH, 280 m; and PL, 786 m. We set transect lines, which ran up and down the stream, in sections of the habitat where the most owl droppings, pellets, and prey remains were found. The time spent censusing prey species in each stream habitat were: LR, 20.0 hr; HR, 7.4 hr; RN, 0.8 hr; SH, 8.0 hr; and PL, 7.8 hr. Relatively little time was spent sampling run habitat because of the few prey detected and the small amount of this habitat in the study area. Nocturnal sampling of prey was conducted from January-June 1994 and from December 1994-July 1995. To estimate the relative abundance of each common prey species, we summed the product of prey abundance in each stream habitat type multiplied by the proportion of the total length covered by each habitat type. To determine the total length of each stream habitat type, we classified segments at 10 m intervals; we established a perpendicular transect across the stream for 4.9 km section, in a part of the study area where we found prey remains. Along the transects across the stream, we recorded the habitat type at each 1-m increment. The total length of each habitat type was calculated as the percentage of all sample points that fell in each type.

Most values reported are expressed as a mean \pm SD. The goodness-of-fit test (Conover 1980) was used to determine if there were differences in prey selection relative to prey availability, season or year. If we found overall differences, we further analyzed the data following procedures described by Neu et al. (1974) to evaluate the extent to which prey were used (observed) relative to their availability (expected). All analyses were performed

using SPSS/PC+ Versions 6.0 and 7.5 (Norusis 1993). Alpha levels were set at $\alpha = 0.05$ for all analyses.

RESULTS

We collected 149 Tawny Fish-Owl pellets in 1994– 95 and 86 in 1998–99. Most pellets (N = 156, 66.4%) were found on rocks (sometimes on logs) in Sakatang Stream. In addition, 69 pellets (29.4%) were collected under 11 frequently-used, streamside resting/foraging sites with perch branches, likely used for hunting, and 10 pellets (4.2%) were found beneath one daytime roost. When trees or branches with vantage points that could be used for hunting were limited, rocks were used as pellet disposition sites.

Altogether, 1239 prey items were identified (Table 2). On average, each pellet contained 5.6 \pm 3.0 prey individuals (range = 2–18). The total estimated biomass of the prey represented in a given pellet ranged from 30.4–268.5 g and averaged 113.8 \pm 52.2 g. Prey included five species of crustaceans, four species of amphibians, one species of fish, one species of rodent, one species of bird, and two species of insects. Nearly all prey species were aquatic (>98% of the individuals; >95% of the total biomass). Crustaceans were taken most frequently (>68%), followed by amphibians (15–25%), and fish (<7%). In terms of biomass, owls consumed mainly crustaceans (40–69%) and amphibians (37–41%).

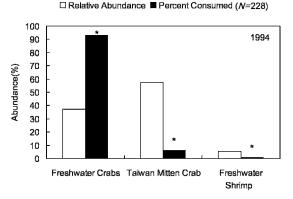
In terms of numbers, the proportion of different prey species in the Tawny Fish-Owl diet varied significantly between years ($\chi^2 = 40.8$, df = 6, P = 0.0001; Table 2). The proportion of the owls' diet comprised of Taiwan mitten crabs (*Eriocheir formosa*) was greater in 1998–99 than in 1994–95. In contrast,

		1994–95	95			1998–99	66-1			TOTAL	TAL	
PREY	Perc Number Frequ	Percent Frequency	ENT JENCY BIOMASS	PERCENT BIOMASS	NUMBER	Percent Frequency	BIOMASS	PERCENT BIOMASS	NUMBER	Percent Frequency	BIOMASS	Percent Biomass
Crustaceans												
Freshwater crabs ^a	479	62.8	2201	17.8	307	64.5	1610	18.8	786	63.4	3811	18.2
Taiwan mitten crab	41	5.4	2798	22.7	60	12.6	4197	49.0	101	8.2	6995	33.5
Freshwater shrimp ^b	39	0.4	41	0.4	5	0.4	27	0.3	5 C	0.4	68	0.3
Anurans												
Taiwan common	83	10.9	3553	28.8	49	10.3	1755	20.5	132	10.7	5308	25.3
toad												
Brown tree frog	45	5.9	835	6.8	9	1.3	91	1.1	51	4.1	926	4.4
Tip-nosed frog	49	6.4	1165	9.5	18	3.8	315	3.7	67	5.4	1480	7.1
Japanese tree frog	8	1.0	27	0.2	2	0.4	6	0.1	10	0.8	32	0.2
Fishc	44	5.8	1173	9.5	28	5.9	562	6.5	72	5.8	1735	8.3
Rodents ^d	60	0.4	495	4.0	0	0.0	0	0.0	60	0.2	495	2.4
Insects ^e	7	0.9	16	0.1	4	0.8	8	0.1	11	0.9	24	0.1
Birds	1	0.1	30	0.2	0	0.0	0	0.0	1	0.1	30	0.2
Total pellets (No.)	149				86				235			

c Kooye minnow (Variarhinus barbatulus).
^d Spinous country rat (Niviventer caxinga).
^e Tettigoniidae, Lucanidae.

The diet of Tawny Fish-Owls living along Sakatang Stream, Taiwan, in 1994-95 and 1998-99. Table 2.

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□ Relative Abundance ■ Percent Consumed (N=294)

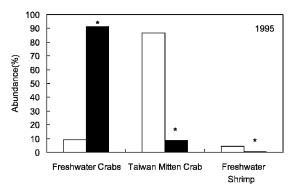


Figure 2. Crustacean prey selection by Tawny Fish-Owls living along Sakatang Stream, Taiwan, in 1994–95. The relative abundance of prey was determined by the number of individuals of each prey counted on prey transects (see Methods). Asterisks indicate the owls caught significantly more or less of the prey than expected (Bonferroni *Z* test, P < 0.05).

the proportion of the owls' diet comprised of brown tree frogs (*Buergeria robustus*) and tip-nosed frogs (*Rana swinhoana*) was greater in 1994–95.

Three species of small freshwater crabs (mass = 4.9 ± 2.4 g, N = 45) were the most common prey species (4.2 crabs per pellet, SD = 2.6, range = 1–15; Table 2). The Taiwan mitten crab (mass = 118.2 \pm 53.3 g, N = 36) was the next most frequently taken crustacean (1.1 crabs per pellet, SD = 0.4, range = 1–3), but it accounted for 33.5% of total prey biomass consumed. Freshwater shrimp (mass = 10.1 \pm 4.9 g, N = 20) were taken occasionally. Tawny Fish-Owls consumed different proportions of crustacean prey than expected based on their abundance in both 1994 ($\chi^2 = 154.2$, df = 2, P = 0.001) and 1995 ($\chi^2 = 132.4$, df = 2, P = 0.001;

Fig. 2). Compared to other crustaceans, small freshwater crabs and Taiwan mitten crabs were taken slightly more often than expected (Bonferroni Z test, P < 0.05), while shrimp were taken significantly less often than expected (P < 0.05).

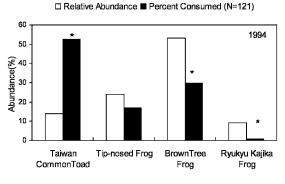
The Taiwan common toad (Bufo bufo gargarizans; mass = 36.0 ± 35.1 g, N = 41) was the most frequently taken amphibian prey (1.3 \pm 0.6 per pellet, range = 1-4) and the second most important species by mass (Table 2). Tip-nosed frogs (mass = 25.2 ± 11.3 g, N = 56) and brown tree frogs (mass = 14.0 \pm 10.0 g, N = 71) were caught frequently. Tawny Fish-Owls consumed significantly more anuran prey than expected based on their abundance in both 1994 ($\chi^2 = 65.8$, df = 3, P = 0.001) and 1995 ($\chi^2 = 58.1$, df = 3, P = 0.001; Fig. 3). Likewise, owls preved on the Taiwan common toad more often than expected (Bonferroni Z test, P < 0.05), but caught the brown tree frog less frequently than expected (P < 0.05; Fig. 3), and the observed versus expected catches of tip-nosed frogs and Japanese tree frogs varied between years (Fig. 3).

The diet of the Tawny Fish-Owl differed significantly among seasons in both 1994–95 ($\gamma^2 = 11.8$, df = 5, P = 0.04) and 1998–99 ($\chi^2 = 33.6$, df = 15, P= 0.004; Table 3). In both sample periods, the proportions of the owls' diet comprised of Taiwan mitten crabs were relatively smaller, and the proportions of other freshwater crabs were relatively higher, in the summer. For amphibians, the proportion of the owls' diet comprised of Taiwan common toads was relatively higher in the winter and spring in the two sample periods. The proportion of the owls' diet comprised of tip-nosed frogs was relatively higher in the winter for both sample periods and was relatively higher in the spring of 1994-95. In addition, brown tree frogs were found in the diet at a relatively higher proportion in the spring in both periods of years and relatively higher in the summer of 1994-95 compared to other seasons.

We found Tawny Fish-Owl belly feathers or down in 17 pellets. The proportion of pellets containing feathers was highest in the fall (80%, N = 10), followed by summer (15.8%, N = 137), winter (3.4%, N = 62), and spring (2.9%, N = 19).

DISCUSSION

In some seasons, the number of pellets collected was small. However, using the running mean method (Kershaw 1964), we found that when more than 15 pellets were sampled from our data, the



□ Relative Abundance ■ Percent Consumed (N=68)

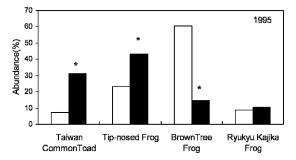


Figure 3. Anuran prey selection by Tawny Fish-Owls living along Sakatang Stream, Taiwan, in 1994–95. The relative abundance of prey was determined by the number of individuals of each prey counted on transects (see Methods). Asterisks indicate the owls caught significantly more or less of the prey than expected (Bonferroni Z test, P < 0.05).

proportions of each prey species in the owls' diet fluctuated within 2%. Because the pellets were collected throughout the year, we believe their contents fairly represent the diet of the Tawny Fish-Owl in different seasons.

The daily intake of the Tawny Fish-Owls calculated from each pellet varied remarkably. An extra, small pellet occasionally produced by owls per day may bias the value of daily intake. We observed feeding of two Tawny Fish-Owls kept in an aviary ($3 \times 2 \times 3$ m) and found they normally produced one and occasionally (2 of 20 d) two pellets (the second one was smaller) per day, 11–17 hr after a meal. We fed these two owls fish, toads, and chicken necks and estimated that their daily food intake averaged 181.2 g (SD = 26.7 g, range = 130–228 g, N = 20 d) and 192.6 g (SD = 37.9 g, range = 140–270 g, N = 20 d). When the small pellets (<130 g of prey biomass) were excluded from calculations of the daily food consumption at the Sakatang Stream, we

estimated the owls actually consumed a mean of 171.9 ± 36.5 g (N = 49) per day, which was close to the daily food intake in captivity.

The daily food intake of Tawny Fish-Owl was 8% of its mean body mass $(2315 \pm 201.6 \text{ g}, N = 8)$, which is about half of that (16%) of the Eurasian Eagle-Owl (Bubo bubo; 0 = 2665 g) in captivity (Mikkola 1983). Eurasian Eagle-Owl eats mostly mammals and birds (Mikkola 1983). We believe the lower intake rate of the Tawny Fish-Owl is not explained by its diet of aquatic prey. Aquatic animals, including fish, crabs, shrimp, and frogs, have fewer calories per unit body mass than mammals and birds because they are lower in fat (Taiwan Department of Health 1991). This means that Tawny Fish-Owl may even have to eat more, rather than less, aquatic prey compared to terrestrial prey to meet its daily energy requirements. Furthermore, the fish-owl is 13.1% smaller than Eurasian Eagle-Owl, and food intake rate is inversely related to the size of Eurasian owls (Mikkola 1983). We suggest that the Tawny Fish-Owl's subtropical distribution may best explain its lower daily intake rate. Kendeigh (1976) pointed out that House Sparrows (Passer domesticus) from the north temperate region have double the daily energy requirements of their Neotropical counterparts.

In a previous study, radio-tagged Tawny Fish-Owls were found mostly at or near streams (Sun et al. 2000). Previous studies and anecdotes indicated that Tawny Fish-Owls preyed primarily on fish (Baker 1927, Fogden 1973, Meyer de Schauensee 1984, Ali 1986, Voous 1988, Mark et al. 1999). However, we found that fish were a minor component, in number and biomass, of the Tawny Fish-Owl diet. The foraging success of Blakiston's Fish-Owl (Ketupa blakistoni) was lower when attempting to capture fish (45-50%) than when hunting for frogs (95%; Yamamoto 1989). In the past several decades, fish populations in the rivers and streams of Taiwan have declined due to deforestation, agricultural practices, pollution, and illegal fishing (Tzeng 1990). If fish were more abundant, they might constitute a larger proportion of the Tawny Fish-Owl's diet. Fish were probably a significant part of the diet of Tawny Fish-Owls living along Nanshih Stream, where five fish farms were established in two owl territories. These fish farms, which raised California rainbow trout (Oncorhynchus mykiss) and ayu (Plecoglossus altivelis), lost 69 fish in July 1994 and 135 fish in June 1995 to Tawny Fish-Owls (Sun et al. 2004).

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		WIN	TER	SPR	ING	SUM	IMER	F	ALL
YEAR	Prey	N	$\%^{\mathrm{a}}$	N	%	Ν	%	Ν	%
1994–95									
	Crustaceans								
	Freshwater crabs ^b	92	62.6	367	62.2	20	76.9	c	_
	Taiwan mitten crab	10	6.8	30	5.1	1	3.8	_	_
	Freshwater shrimp ^d	0	0.0	3	0.5	0	0.0	_	_
	Anurans				0.0				
	Taiwan common toad	23	15.6	58	9.8	2	7.7	_	_
	Brown tree frog	4	2.7	39	6.6	2	7.7	_	_
	Tip-nosed frog	9	6.1	39	6.6	1	3.9	_	_
	Japanese tree frog	1	0.7	7	1.2	0	0.0	_	_
	Fishe	7	4.8	37	6.3	0	0.0	_	_
	Rodents ^f	0	0.0	3	0.5	0	0.0	_	_
	Insectsg	1	0.7	6	1.0	0	0.0	_	_
	Birds	0	0.0	1	0.2	0	0.0	_	_
	Total prey items	147		590		26		_	_
	Total pellets	28		118		3		_	_
1998–99	-								
	Crustaceans								
	Freshwater crabs	100	56.5	51	58.0	84	73.0	72	64.3
	Taiwan mitten crab	24	13.6	15	17.0	8	7.0	13	11.6
	Freshwater shrimp Anurans	0	0.0	2	2.3	0	0.0	0	0.0
	Taiwan common toad	22	12.4	11	12.5	11	9.6	5	4.5
	Brown tree frog	0	0.0	3	3.4	2	1.7	1	0.9
	Tip-nosed frog	15	8.5	1	1.1	2	1.0	0	0.0
	Japanese tree frog	13	0.6	1	1.1	0	0.0	0	0.0
	Fish	13	7.3	4	4.6	8	7.0	3	2.7
	Rodents	0	0.0	0	0.0	0	0.0	0	0.0
	Insects	2	1.1	0	0.0	0	0.0	2	1.8
	Birds	0	0.0	0	0.0	0	0.0	0	0.0
	Total prey items	177	0.0	88	0.0	115	0.0	96	0.0
	Total pellets	34		19		115		17	

Table 3. The diet, by season, of Tawny Fish-Owls living along Sakatang Stream, Taiwan, in 1994–95 and 1998–99.

^a Frequency (%).

^b Three species (Candidiopotamon spp.).

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° —No data.
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^d Macrobrachium sp.

e Kooye minnow (Varicorhinus barbatulus).

f Spinous country rat (Niviventer coxinga).

g Tettigoniidae, Lucanidae

Larger owl species tend to take larger prey (Marti 1974). Indeed, Tawny Fish-Owls preyed heavily on the large Taiwan common toad even though it was much less abundant than the brown tree frog and the tip-nosed frog. The Taiwan common toad is the largest and least agile anuran living along Sakatang Stream. Tawny Fish-Owls apparently had no problem with the toad's poison gland. Toads were also eaten by Blakiston's Fish-Owl on the Bikin River, Russia (Pukinskiy 1973).

Tawny Fish-Owls took freshwater crabs and the Taiwan mitten crab more often than expected. The crabs were much slower than freshwater shrimp, which were preyed upon less frequently than expected. The shrimp waved their long, sensitive antennae above their head, which may have given them an instant to detect and escape from attacking owls. In this study, our sampling of prey abundance may be biased due to the selective placing of transect lines in stream sections the owls visited most often. Thus, our results may not apply to populations of Tawny Fish-Owls elsewhere.

The breeding activity of at least some prey species may influence their consumption by Tawny Fish-Owls. From late June-October, female freshwater crabs (C. rathbunae) temporarily leave the water and breed in the riparian forest (Liu and Li 2000); during this period owls consumed proportionally more freshwater crabs. This movement for breeding may increase the chances of freshwater crabs being taken by owls. Each spring, Taiwan mitten crab, a catadromous species, starts to migrate to an estuary to breed. The adults die after breeding, but young crabs will not move upstream until the fall, 2 yr later (Hung 1993, Chan 2000). This may be the reason why the Taiwan mitten crabs were infrequently consumed by the owls in the summer, when the crab's abundance is lowest because it is in the interval between emigration and recruitment. Amphibians may suffer higher predation during their breeding season. A slightly greater number of brown tree frogs were caught by owls during the frogs' spring and summer breeding season than in other seasons (Lin 2001). The Taiwan common toad and tip-nosed frog breed in winter (Li 1986, Kam et al. 1998), and this was when the proportion of these species in the Tawny Fish-Owl diet was relatively high. Breeding female frogs and toads leave the forest and spawn in the stream. Females are heavy with eggs, reducing their agility and possibly increasing their vulnerability to predators. Males also are probably more likely to be caught during mating.

Grebes (*Podiceps* spp.) swallow their feathers, which accumulate between the gizzard and intestine, to entangle sharp fish bones and indigestible remains, facilitating bolus regurgitation (Gill 1997). In our study, just five of 35 Tawny Fish-Owl pellets containing fish, and 16 of 204 pellets containing crabs, also contained owl feathers. We observed captive owls and found that wet feathers readily stuck to their bills while preening, especially during the peak molting of body feathers in the fall. Therefore, we propose Tawny Fish-Owls consume their own feathers accidentally and do not intentionally ingest feathers to aid in regurgitation.

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