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NEST PROVISIONING OF THE ORIENTAL HONEY-BUZZARD (*PERNIS PTILORHYNCUS*) IN NORTHERN TAIWAN

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Raptors in the genus *Pernis* have a unique diet consisting primarily of the larvae, pupae, and adults of social Hymenoptera (Clark 1994, Orta 1994, Bijlsma 1999, Gamauf 1999). The European Honey-buzzard (*P. apivorus*) has been studied in some detail (Kostrzewa 1987a, 1987b, 1987c, Steiner 1992, Saporetto et al. 1994, Selas 1997, Van Manen 2000), but the biology of the Oriental Honey-buzzard (*P. ptilorhynchus*) has not been studied in depth (Clark 1994, Orta 1994, Morioka et al. 1995).

Based on our monthly raptor surveys in northern Taiwan's Yangmingshan National Park (25°10'N, 121°33'E) between 1993 and 2003, the Oriental Honey-buzzard was a common spring and autumn migrant, a rare winter visitor, and an uncommon summer resident. We found one Oriental Honey-buzzard nest in 1994 and one in 1999.

This paper reports the composition, seasonal variation, and relative importance of the prey species provisioned to the nest in 1999 and compares the male and female contributions to the nestling.

METHODS

We constructed a hide eye-level with the nest on a steep slope about 30 m away. We monitored the nest provisioning of the parents and recorded the time and the gender each time an adult returned to the nest. The male could be distinguished based on an orange-brown iris and broader dark tail bands, while the female has a yellow iris and narrower dark tail bands (Morioka et al. 1995). We simultaneously videotaped the nest-provisioning events. From these videotapes, we identified prey by comparing these with reference specimens in terms of structure, shape, color, and size of the wasp nests, the color and placement of the stem of the wasp nests, and

the color of the seal on cells containing pupae. Observations were made from 12 July–19 August, the day before the nestling fledged.

Because it was impossible to determine the exact sizes of the wasp nests from the videotapes due to filming angles, we collected empty wasp nests discarded under the honey-buzzard nest for species identification and counted the number of cells per wasp nest. Based on the sizes of these wasp nests, we categorized all the wasp nests in the videotapes into small, medium, or large classes (Table 1).

To understand the relationship between wasp activity and prey capture rate, we identified the paper wasps active in July and August. We searched for wasp nests along three trails in the study area through wooded areas with small cabins, each 1 km in length. We scanned the vegetation from canopy to the shrub layer and checked buildings carefully. Each transect line was searched at least twice to ensure the discovery of all wasp nests. For each wasp nest found, we measured height above ground, its length and width, recorded the number of cells, and described its shape. We collected one actively-used nest for each species found in order to obtain the proportion of cells occupied by eggs, different larval instars and pupae, and measured the mass of larvae at each instar.

Biomass per wasp nest was calculated with the following equation: Biomass = the number of cells/nest × proportion of cells occupied × the mean biomass/larva. The number of cells found on each wasp nest was related to size (Table 1). We used the wasp nests we collected as standards to determine cell occupancy and larval mass. Biomass estimates of reptiles and frogs were based on the mean mass of >10 individuals per species caught in the study area.

RESULTS

Food Composition and Seasonality. We observed the honey-buzzard nest for 26 d (204.7 hr) and recorded 123 food items delivered by parents. Among these, 78.9% were complete wasp nests ($N = 97$), 16.3% were Swinhoe's brown frogs (*Rana swinhoana*; $N = 20$), and 4.9%

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Table 1. Wasp nest-size classes and their cell numbers.

SPECIES	SIZE RANK	CELL NUMBER
<i>Polistis tenebriocosus</i>	Small	<39
	Medium	40–69
	Large	>70
<i>Polistis rothneyi</i>	Small	<119
	Medium	120–219
	Large	>220
<i>Polistis gigas</i>	Small	10–19
	Medium	20~29
	Large	>30
<i>Polistis</i> sp. <i>Parapolybia varia</i>	Medium	780
	Small	<179
Unidentified wasp comb (<i>Po. tenebriocosus</i> or <i>Po. rothneyi</i>)	Medium	180–349
	Large	>350
	Small	60
	Medium	80
	Large	100

were yellow-mouthed japalura lizards (*Japalura polygonata xanthostoma*; $N = 6$). All 97 wasp nests belonged to paper wasps (Polistinae, Vespidae), but two belonged to an unknown species and 24 could not be distinguished between *Po. tenebriocosus* and *Po. rothneyi* because either the nestling blocked the camera or the speed of delivery was too rapid. Among prey items that could be identified, *Po. tenebriocosus* nests ($N = 36$) constituted 29.3%, *Po. rothneyi* 13% ($N = 16$), *Po. gigas* 9.8% ($N = 12$), *Parapolybia varia* 5.7% ($N = 7$), and *Polistis* sp. 1.6% ($N = 2$). The frequency distribution of wasp nests brought back to the nestling was not different from those found along our transect lines (nests recorded: 29, *Po. tenebriocosus* = 21, *Po. rothneyi* = 3, *Po. gigas* = 2, and *Pa. varia* = 3, *Polistis* sp. = 0, $\chi^2 = 5.657$, $df = 4$, $P > 0.05$).

The body sizes of these five species of paper wasps varied from the world's largest paper wasp (*Po. gigas*; 4.5 cm for adult males) to a new species, *Polistis* sp. (1.3 cm). The colony sizes of these wasps also varied from 12 cells in a *Po. gigas* nest to more than 400 cells in a *Pa. varia* nest. Based on biomass estimates from the nests we collected, we found that the pupae and the fourth and fifth instars of *Po. tenebriocosus*, *Po. rothneyi*, *Po. gigas*, and *Pa. varia* constituted 93.4%, 95.4%, 95.7%, and 87.6% of the total biomass of a nest, and occupied 44%, 45%, 56%, and 39.6% of the cells, respectively. We did not find any nests of the new *Polistis* sp. to obtain larva/pupa mass measurements. Because nests of this species were brought back only twice during the entire study period, we decided not to include this species in our biomass calculations.

Considering the cumulative biomass of all prey types delivered to the honey-buzzard nest, frogs and lizards together made up 16.9%, while Polistinae wasps made up

Table 2. Relative biomass of different prey types brought to the Oriental Honey-buzzard nest in northern Taiwan.

SPECIES	TOTAL BIOMASS (g)	PERCENT
<i>Polistis tenebriocosus</i>	1003.00	31.59
<i>Po. rothneyi</i>	689.34	21.71
<i>Po. gigas</i>	244.50	7.70
<i>Parapolybia varia</i>	90.84	2.86
Unidentified nests ^a	611.16	19.25
Frogs	500.00	15.75
Lizards	36.00	1.13
Total	3174.84	100.00

^a Either *Po. tenebriocosus* or *Po. rothneyi*. We calculated the biomass by using the mean mass and mean cell occupancy of the two species.

83.1% (Table 2). Frogs were delivered in July and early August, and lizards were delivered in July only. By mid-August, honey-buzzards provisioned only paper wasps (Fig. 1). The patterns of seasonal variation were similar by prey frequency and by biomass. The biomass delivered to the nest per hour of observation fluctuated between 5–40 g throughout the nestling period except on the third d before fledging (Fig. 2). We did not monitor the nest on 18 August and so were unable to determine if this increased rate of prey delivery took place two consecutive days before fledging.

Paper Wasp Nest Height Distribution. The 29 paper wasps nests we found along trails hung from vegetation ($N = 10$) or eaves ($N = 19$) from 0.5–11.5 m above the ground. More than 86% were between 0.5–4 m high, the remaining four nests were above 6 m (3 *Po. tenebriocosus* and 1 *Po. rothneyi*).

Sexual Differences in Contribution. The male made

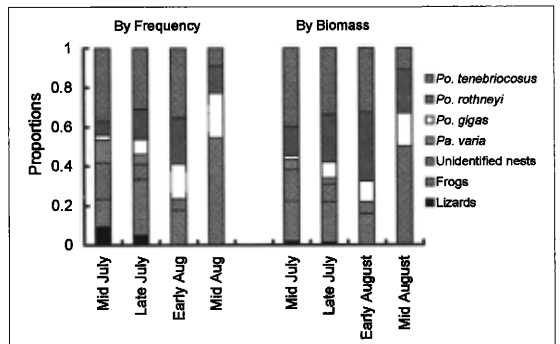


Figure 1. Diet of Oriental Honey-buzzard nestling based on the frequency of prey deliveries to the nest. Paper wasps in diet included: *Polistis tenebriocosus*, *Po. rothneyi*, *Po. gigas*, and *Parapolybia varia*.

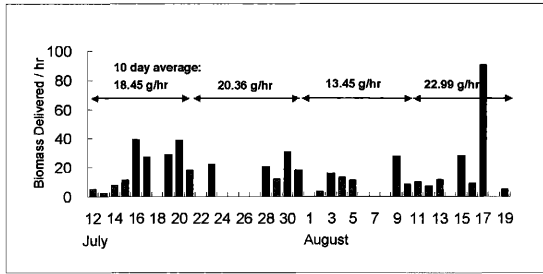


Figure 2. Biomass delivered to an Oriental Honey-buzzard nest in northern Taiwan per hour of observation. The nestling fledged on 20 August. The mean biomass delivered per hour for each 10-d period is given at the top of the histogram.

49.6% of the visits and the female 29.3%; the sex was uncertain in the remaining visits. Among the biomass delivered by adults of known sex, the male contributed 56% and the female 44% in July and in early August. After 9 August, female contribution ceased completely. The difference in biomass contribution between sexes across time periods was significant ($\chi^2 = 305.31$, $P < 0.0001$). Even if all the unknown feedings were made by the female, the male still would have contributed more biomass than the female during the final 10 d before fledging.

DISCUSSION

Prey Choice. Oriental Honey-buzzards captured prey that were on the ground, such as frogs in the shrub layer, or in the sub-canopy paper wasp nests. The pair we studied in Yangmingshan primarily brought *Polistes* nests as food for their young. Among known wasp prey, the frequency of different species of wasp nests they brought to the nestling was proportional to those available in the environment. However, they ignored the nests of the small paper wasp, *Po. takasagonus*, even though these nests were as common as the *Po. tenebriocosus* nests along our transect lines. A colony of *Po. takasagonus* was constructing a nest just below the honey-buzzard nest, but the honey-buzzards never showed interest in it. The biomass of the largest *Po. takasagonus* nest we found weighed less than 9 g, less than the smallest nest brought back by parents (9.91 g). There may be a minimum-size threshold for a wasp nest to be energetically profitable for honey-buzzards.

Another potential prey are *Vespa* hornets (Vespidae, Vespinae), which are large, conspicuous, and usually number by the hundreds per colony. The nests of some species are built on high branches and can be as large as 60 cm in diameter (M.C. Kuo pers. comm.). Hornets and wild bees (Apidae) were active within the home range of the honey-buzzard pair, but the nests of these families were never delivered to the nestling.

The honey-buzzards' food choice was most likely influ-

enced by the accessibility of prey and its energy content in relation to the handling cost. Hornets are aggressive and usually defend their combs vigorously (Evans and Eberhard 1970, Kuo and Yeh 1987). Ranking the aggressiveness of wasps into five classes (1 being most aggressive), *Po. tenebriocosus* and *Po. gigas* would be in class 5, *Po. rothneyi* and *Pa. varia* in class 3, while the *Vespa* species would be in classes 1–3 (Kuo and Yeh 1987). Although the stomach contents of European Honey-buzzards contained small numbers of hornets (Loskutova 1985), and adult Oriental Honey-buzzards probably consume hornets, preying on hornet nests no doubt demands a high energy cost. Specifically, honey-buzzards would need to evade the attack of a large number of hornets and would have a high risk of injury.

Wild bees are common in Taiwan, but most nest in rock crevices and tree cavities (Kuo and Yeh 1987). Polistinae nests in Taiwan always hang by a stem, which makes them easy for honey-buzzards to remove in flight. When paper wasps are abundant, there should be little incentive for a honey-buzzard to open logs or remove rocks to access a bee nest.

Seasonal Variation in Prey Composition. Paper wasps in Taiwan generally establish colonies in late April or May, and colony expansion usually occurs in June and July, followed by a mating period in July or August before they enter the dormant wintering stage, when breeding and foraging activities cease (Kuo and Yeh 1987, Lu et al. 1992). Based on this chronology, wasp nests would be small in the early part of the breeding season (July). During this period, the Oriental Honey-buzzards delivered wasp nests to the nestling and supplemented the nestling's diet with frogs and lizards. By mid-August, although frogs and lizards were still common, wasp colonies were large and the honey-buzzards delivered only paper wasp nests. European Honey-buzzards also foraged almost entirely on wasp nests when wasps were available (Martin 1992, Ferguson-Lee and Christie 2001).

European Honey-buzzards find wasp nests by watching the insects return from foraging trips (Grigor'yev et al. 1977, Martin 1992, Ferguson-Lee and Christie 2001). We do not know if Oriental Honey-buzzards could determine whether a wasp was departing from or returning to its nest. However, by following a flying wasp, honey-buzzards could either find the wasp foraging or come upon a nest.

Timing of Breeding. If the two nests we found are typical for this species, the Oriental Honey-buzzard has a much later breeding season than the other species of raptors in Taiwan. The hatching of eggs in July appears to be timed with the increase of paper wasp colonies in our study area. The delayed onset of its breeding season could result from the unavailability of wasp nests earlier in the spring. Wasp abundance has been known to influence the breeding success of European Honey-buzzards (Kostrzewa 1987c, Saporetti et al. 1994, Steiner 2000).

Sexual Differences in Provisioning. From mid-July to early August, the female Oriental Honey-buzzard contrib-

uted more than 30% of the biomass delivered to the nestling, and the male at least 40%. After 9 August, the female's contribution ceased completely even though she remained in the vicinity of the nest. Using a modeling analysis, Brodin et al. (2003) showed that whether a female raptor assisted with hunting for the young late in the nestling period depended on the hunting success of the male, environmental conditions, and the energy demands of the young. Because the pair of honey-buzzards we monitored had only one nestling, perhaps the male alone could provide sufficient prey for the young (reported clutch size for Oriental Honey-buzzard is two eggs; Sung et al. 1991).

Our study advanced what was known about Oriental Honey-buzzard. We found that adults primarily brought paper wasps as prey for their nestling, and the frequency of each species of wasp nest brought back reflected prey availability. Low energetic profitability most likely made some species of wasp nests undesirable. In addition, our results from one nest showed that the female delivered food less often and contributed less biomass to the nestling than the male.

RESUMEN.—Se conoce muy poco sobre la ecología y el comportamiento de *Pernis ptilorhyncus*. Con base en censos realizados entre 1993 y 2003, se determinó que esta especie es un visitante poco común durante el verano en Yangmingshan, Taipei, Taiwan. Encontramos un nido en 1994 y otro en 1999. A través de observaciones directas y de grabaciones de video realizadas en 1999, registramos las presas llevadas al nido durante 26 días, entre el 12 de julio y el 19 de agosto ($N = 204.7$ hr, $N = 123$ presas). Nuestros resultados revelaron que el 78.9% (83.7% en términos de biomasa) de los ítems alimenticios fueron nidos de avispas, el 16.2% (15.3% en biomasa) fueron ranas y el 4.9% (1.1% en biomasa) fueron lagartijas. Cinco especies de avispas que construyen nidos de papel fueron identificadas: *Polistes tenebriocosus*, *Po. rothneyi*, *Po. gigas*, *Parapolybia varia* y *Po. sp.* Las ranas y lagartijas fueron registradas sólo entre el 12 de julio y el 10 de agosto. La dieta de la cría de *P. ptilorhyncus* reflejó la fauna disponible de avispas y el ciclo anual de éstas en el área de estudio. Los machos y hembras no contribuyeron igualmente a alimentar a su cría. Las hembras dejaron de llevar alimento diez días antes de que el pichón abandonara el nido.

[Traducción del equipo editorial]

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WINTER DIET OF THE GREATER SPOTTED EAGLE (*AQUILA CLANGA*) IN THE AMVRAKIKOS WETLANDS, GREECE

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KEY WORDS: *Greater Spotted Eagle*; *Aquila clanga*; diet; winter; wetland; Amvrakikos; Greece.

The Greater Spotted Eagle (*Aquila clanga*) is a globally-threatened raptor, which breeds from Eastern Europe to the Pacific coast of the northern Far East and winters locally in southern Europe, Asia, the Middle East, and sub-Saharan Africa as far south as Uganda and Kenya (Tucker and Heath 1994). The main reasons for its decline are habitat destruction and degradation (in both forests, where the species nests, and wetlands, where it forages), disturbance during the breeding season, illegal shooting (mainly in migration), and to a lesser extent, nest robbing (Tucker and Heath 1994, Meyburg et al. 2001). The primary proposed conservation measures include the establishment of protected areas in the breeding habitat of the species, preservation of a mosaic of breeding-feeding habitat, protection of wetlands, avoidance of disturbance during the breeding season within 300 m of nests, as well as improvement of legislation,

international cooperation, monitoring, and research (Meyburg et al. 2001). The biology of the Greater Spotted Eagle has not been examined to a great extent; additionally, its diet has been examined almost exclusively during the breeding season (e.g., Priklopsky 1960, Galushin 1962, Pankin 1972, Ivanovsky 1996). Few studies of any kind have been conducted in the winter quarters of this species (Moltoni 1943, Francois 1992, Qingxia 1996)

Although an important population of Greater Spotted Eagles winters in the extensive wetlands of northern and central Greece (45–85 individuals), up to now it has received very little attention (Hallmann 1989, Handrinos and Akriotis 1997). Here, we present the results of an examination of Greater Spotted Eagles at a key wintering site, the Amvrakikos wetlands, western Greece, where up to 12 individuals winter each year.

STUDY AREA AND METHODS

Our study area was in the Amvrakikos wetlands, western Greece (38°59'–39°11'N, 20°44'–21°07'E). Amvrakikos is a Ramsar Wetland, a Special Protection Area, and proposed National Park. It is one of the largest wetlands in Greece covering 220 km² including river deltas, coastal

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