well-corroborated phylogeny for the Thamnophilinae. Nevertheless, *Xenornis setifrons* and the allopatric, sibling species pair of *Thamnomanes caesius* and *T. schistogynus* appear to be ecological counterparts, sharing a niche rare within the Thamnophilinae.

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PREY TRANSPORT BY LOGGERHEAD SHRIKES[1]

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Key words: Foraging; Loggerhead Shrike; Lanius ludovicianus; *prey transport; Florida.*

Recent studies demonstrate that avian single-prey loaders preferably transport larger prey to their nests (e.g., Gronlund et al. 1970, Carlson 1985, Krebs and Avery 1985, Sonerud 1989). For central-foraging predators that carry prey for further handling and caching or for feeding of mates or young, the value of the prey is influenced by the energetic cost of transport (Orians and Pearson 1985).

Shrikes (Laniinae) are birds of open-savannah habitats that exhibit central-place foraging and caching behavior. Northern Shrikes (*Lanius excubitor*) transport whole arthropods and reptiles to the nest, but decapitate mammalian prey (Gronlund et al. 1970). This species usually transports a higher-than-optimal load size, compared to other avian predators such as the Eurasian Kestrel (*Falco tinnunculus*) (Sonerud 1989). Sonerud (1989) reasoned that the optimal load-size carried by a Northern Shrike made up a higher percent of the body mass than it did for a Kestrel, because the relative cost of flying increases with increasing body mass. Sonerud also found that central-place foraging birds which differed in size and exploited the same prey type, differed in their selection of prey for transport over the same distance. Carlson (1985) found that Red-backed Shrikes (*Lanius collurio*) delivered to females prey collected close to the nest; he reasoned that the range of prey sizes economically worth returning decreased with distance and, inversely, the range of prey sizes available for self-feeding increased with distance.

Studies of hunting by Loggerhead Shrikes (*Lanius ludovicianus*) are limited to foraging behavior (e.g., Bohall-Wood 1987), prey selection (e.g., Kaufman 1973), and reproductive requirements and capabilities (e.g., Kridelbaugh 1982, Novak 1989), and opportunistic observations wherein large prey are reported (e.g., Balda 1965). Shrikes are reported carrying prey of approximately their own body mass in their feet (e.g., Conley 1982, Ingold and Ingold 1978), and carrying smaller prey in their beaks (e.g., Chapman and Casto 1972). However, mode of prey transport and distance flown with prey as functions of prey body mass are unstudied.

The Loggerhead Shrike (mean body mass on study site 47.9 ± 3.3 SD, $n = 103$) is an exclusive carnivore. Because prey carried in the bill should destabilize a flying bird and consequently increase energetic costs, I postulated that to maintain a more stable center of gravity, prey items weighing more than some threshold value would be carried in the feet rather than in the bill.

I studied post-breeding Loggerhead Shrikes during October–December 1991 at the 4,300 ha MacArthur

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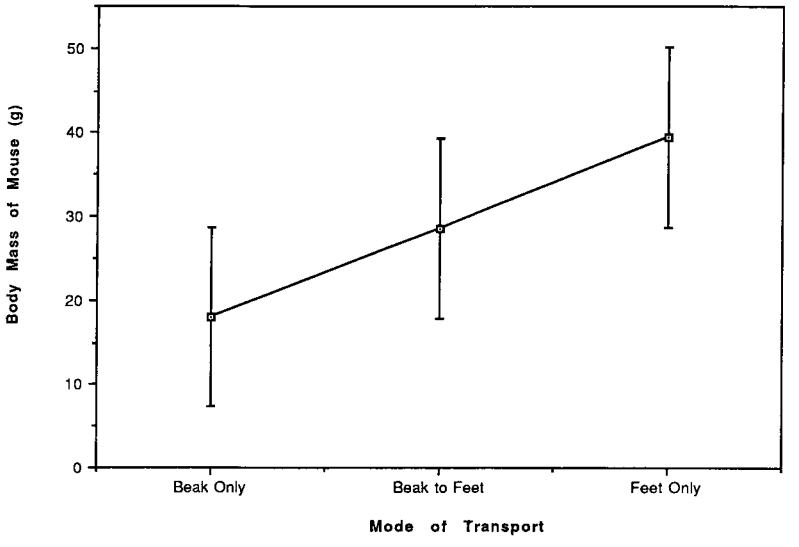

FIGURE 1. Mode of transport of 78 house mice by 23 Loggerhead Shrikes. The boxes indicate average body mass of mice, and error bars indicate the standard deviation.

Agro-ecology Research Center of the Archbold Biological Station, Lake Placid, Florida. I captured territorial shrikes in composite treadle/bal-chatri traps (Yosef and Lohrer 1992) and banded them for individual recognition with the United States Fish and Wildlife Service aluminum bands and color bands, and used the shrikes' aggressive responses to playbacks and taxidermic mounts to map the borders of all territories on the ranch.

I offered 23 individual shrikes laboratory mice (*Mus musculus*) ranging in size from 9.0 to 61.9 g. All mice ($n = 78$) were weighed on a Acculab electronic digital scale (±0.1 g). Distances were measured with optical range finders (Ranging Inc., models 120 and 620, accuracy ±2%). For the birds' initial flight with the prey, I recorded the mode of transport (beak, feet, beak to feet while in flight) and distance flown.

The average initial distance flown with prey in the beak only was 6.4 m, in beak and feet 4.8 m, and in feet only was 4.5 m (Table 1). Body mass of prey significantly affected mode of transport (Factorial analysis of variance, $F = 17.78$, 2 df, $P = 0.0001$, Fig. 1), and distance flown with prey after being disturbed (Factorial ANOVA, $F = 5.92$, 2 df, $P = 0.051$), however, it did not affect the overall initial distance flown after retrieving the mouse (Factorial ANOVA, $F = 0.512$, 2 df, $P = 0.7738$). Using the Fisher Planned Least Significant Difference Test, significant differences were found at the 95% level between the modes of transport (beak only vs. beak and feet = 4.1; beak only vs. feet only = 3.4; beak and feet vs. feet only = 3.7). Average body mass of prey transported in the beak only was 18.3 ± 7.5 g (range 9.0–30.5 g, $n = 22$) and flew an average of 65 m. Shrikes moved prey from beak to feet in 18 instances and average mass of prey was 27.3 ± 3.1 g (range 23.9–36.8 g, $n = 18$), and flew an average of 49 m. Body mass of prey transported only in the feet averaged 39.6 ± 6.9 g (range 29.2–61.9 g, $n = 38$), and flew an average of 35 m.

Results conform with the modes of transport previously reported for free-ranging Loggerhead Shrikes. Prey body mass was significantly related to distance carried. Prey carried in feet ranged from 50 to 129% of the shrike's average body mass. This range includes values for species previously observed transported. Shrikes have been observed in unsuccessful attempts to lift heavy prey with their bills (Balda 1965, Comer and Freeland 1980). Hopkins (1953), Caldwell (1967), and this study contradict Bent's (1950) view that shrikes do not use their feet to transport prey, but depend upon the bill to seize and carry prey. Slack (1975) expected that selection by shrikes would be affected by size of

TABLE 1. The average distance (m) flown by Loggerhead Shrikes using three different modes of transport. (1) denotes beak only, (2) beak and feet, and (3) feet only.

	Avg. body mass (g)	Initial distance ± SD	Range	Disturbed distance ± SD	Range	*n*
1	18.3	6.4 ± 4.2	1–21	64.6 ± 22.2	30–97	22
2	27.3	4.8 ± 2.7	1–9	49.1 ± 28.1	10–58	18
3	39.6	4.5 ± 2.2	1–9	35.1 ± 23.3	8–65	38

the prey. The current analysis indicates that Loggerhead Shrikes will readily attack and carry prey up to at least 129% their own body mass; it is possible that they can carry heavier prey.

Moving of prey from the beak to the feet while in flight was previously reported by Esterly (1917). The current study shows that prey of intermediate mass (50–92% of shrike body mass) are readily carried in the beak during take-off, but apparently are more efficiently transported if moved to the feet. This weight range overlaps that in which shrikes carried their prey in the beak (19–58% of shrike mass) or feet (61–131% of shrike mass). Between the prey mass of 52–60% of shrike mass, however, prey transport usually involved transfer from beak to feet (10 of 11 trials).

The high variation in the results of this study may have been partially influenced by environmental factors (e.g., wind speeds and direction in relation to the bird) that were not recorded, and so could not be treated as covariates in the model. It remains to be determined whether shrikes in varying environmental conditions will change the range of body mass of prey transported as a function of the mode.

It is probable that carrying prey in the feet stabilizes the shrike while in flight and that beyond some threshold mass, prey held in the beak destabilizes the shrike and increases the energetic cost of transport. Thus, small prey are transported in the beak, intermediate prey in beak and then feet, and heavy prey only in the feet.

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