NILSSON, S. G. 1986. Evolution of hole nesting in birds: on balancing selection pressures. Auk 103:432–435.

RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contr. Zool. 9:1–48.

SOKAL, R. R. AND F. J. ROHLF. 1981. Biometry, 2nd ed. Freeman and Co., San Francisco, California.

IVÁN LAZO AND JUAN J. ANABALÓN, *Dept. de Ecología, Universidad Católica de Chile, Casilla 114-D, Santiago, Chile.* *Received 28 Dec. 1989, accepted 15 Sept. 1990.*

Wilson Bull., 103(1), 1991, pp. 146–149

The proximate costs and benefits of polygyny to male Northern Shrikes.—Trivers (1972) defined parental investment as any investment by a parent in an offspring that increases the offspring's chance of surviving at the cost of committing resources to other offspring. Wittenberger (1981) modified this definition to apply to entire clutches or broods of offspring. An exact definition of parental investment has been disputed for some time, and even today the debate continues. Discussions of mating strategies typically deal with the benefits and cost of a behavior to females (e.g., Orians 1969, Alatalo et al. 1986). The consequences for males, however, are less often addressed. For example, polygyny has obvious benefits over monogamy for males because a polygynous male has a greater reproductive potential during a single breeding season. However, polygyny may also impose higher costs to the male if he contributes to the care of offspring. If there is a cost of polygyny to the male it is ultimately paid for in reduced survivorship, which unfortunately is difficult to measure because it requires large sample sizes and long-term studies. But, even proximate measures of cost, such as the time involved in feeding and defending additional young, may be informative because time spent in parental care probably exposes the male to additional hazards of predation and injury (Reid and Sealy 1986). Proximate costs to males might also be relevant to mate selection. In fact, some theories of mate selection assume that females choose among males on the basis of the male's ability to incur proximate costs (Slagsvold 1986, Alatalo et al. 1986).

We investigated some of the proximate costs of polygyny to male Northern Shrikes (*Lanius excubitor*). In Israel, male Northern Shrikes reside permanently in breeding territories. Females are not permanent residents and leave the breeding area immediately after their broods fledge. Seven male Northern Shrikes were observed during the 1987 breeding season, from January to June, at Sede Boqer (34°47′N, 30°52′E, 475 m ASL), in the Negev Desert highlands of Israel. The study area is a flat loessal plain. The plateau supports a sparse dwarf shrub community dominated by *Hammada scoparia, Zygophyllum dumosum, Reaumuria hirtella, Anabasis syriacus,* and *Artemesia herba-alba.* The major woody species are *Tamarix nilotica, Atriplex halimus, Retama raetam,* and *Thymelaea hirsuta.* Regional flora includes a large variety of herbs and geophytes (Danin et al. 1975).

Two of the seven males we observed had polygynous relationships (Yosef and Pinshow 1988b); the first two documented cases of polygyny in this species. Following this discovery, time-budgets were constructed for all seven pairs under observation. The birds' diurnal behavior was divided into the following categories: (1) perching, (2) flying (usually to or from collecting prey, or chasing conspecifics or heterospecifics from the area, or changing lookout points), (3) handling prey (recorded from the instant the shrike landed on or near the prey and attacked it until the prey was impaled or consumed), and (4) preening.

TABLE 1
AVERAGED TIME-BUDGETS AND DIETS OF POLYGYNOUS AND MONOGAMOUS MALE NORTHERN SHRIKES

	Polygynous males (N = 2)	Monogamous males (N = 5)
Time budgets		
Total hours of observation	216.0	186.0
Percent total:		
Perched	82%	69%
Flight	2%	2%
Handling prey	2%	1%
Preening	12%	32%
No. of occasions seen feeding nestlings	0	17
Diets		
Number of prey taken	256	109
Percent total:		
Arthropods	89%	95%
Reptiles	7%	4%
Birds	3%	—
Mammals	0.4%	—
Vertebrates : arthropods ratio	0.12:1	0.04:1

We observed the two polygynous males for a total of 216 h and the five monogamous ones for 186 h on 56 days. All seven males were captured with a bal-chatri noose trap, color-banded and released. Territories were mapped by plotting points of shrike activity and by observing the reaction of the males to taped songs of other males and to a mounted specimen. Birds were sexed by observing mating and other behavior. As far as was possible, all prey taken were identified by observing the birds with the help of binoculars or a telescope, or by inspecting impaling sites. The birds and their mates were observed through a complete breeding season, and clutch size, hatching success, and number of nesting attempts were recorded. Because the exact number of young that fledged from each nest could not be determined, we indexed the seasonal fitness of each male by the total number of eggs laid in nests in his territory. During this stage of the research, it was still unclear why some of the young disappeared from their nests at the very early stage of approximately 10 days of age. It was later determined that parents often transferred their young to the base of neighboring trees or bushes (Yosef and Pinshow 1988a).

We compared polygynous and monogamous males with respect to the time spent in prey detection and handling. Territory quality was the uncontrolled variable. Comparisons between contemporaneous observation periods of fixed length revealed that polygynous males spent significantly more time than monogamous males seeking prey ($Z = 3.74$, $P < 0.0003$, $N = 56$) and handling prey ($Z = 3.92$, $P < 0.0001$, $N = 43$) (Wilcoxon's signed rank test, Steele and Torrie 1980). Males usually brought food to the vicinity of the nest and passed it on to the female or impaled it at cache sites. Females were seen to retrieve such food by themselves. Polygynous males were never seen feeding or attending their young directly, although monogamous males were observed to do so on 17 occasions (Table 1).

Monogamous males caught 0.59 prey per hour (109/186 h), compared to 1.19 prey per

TABLE 2
SIZES OF TERRITORIES, NUMBER OF NESTS AND NUMBER OF EGGS LAID BY MATES OF MALE NORTHERN SHRIKES

	Territories defended (ha)	Number of nestlings	Number of eggs laid
Polygynous males			
#1	76.9	3	16
#2	72.7	4	21
Monogamous males			
#1	54.8	2	11
#2	68.8	1	12
#3	59.2	2	10
#4	55.3	2	10
#5	56.9	2	11

hour (256/216 h) for the polygynous males. The diet of monogamous males consisted mainly of arthropods (95.4%), the rest being lizards (4.6%). Although polygynous males also took mainly arthropods (89.4%), they also hunted a variety of vertebrates including reptiles (7.4%), passerine birds (2.7%) and small rodents (0.4%). A comparison of the arthropod vertebrate ratio shows that polygynous males handled three times as many vertebrates as did monogamous males (0.12:1 vs. 0.04:1).

Polygynous males defended significantly larger territories than did monogamous males (Mann Whitney Test $U_{(0)2,5} = 10$, $P < 0.05$) (Table 2). There was also a significant difference in the total number of nesting attempts during the season for each male: 3.5 ± 0.7 attempts for the polygynous males and 1.8 ± 0.5 for monogamous males ($U_{2,5} = 10$, $P < 0.05$) and the mates of polygynous males laid significantly more eggs (18.5 ± 3.5 vs 9.4 ± 2.5) ($U_{2,5} = 10$, $P < 0.05$).

If all the eggs laid by each female resulted from within-pair copulations, then polygynous males produced nearly twice as many eggs as did monogamous males. However, increased egg production was not without cost: polygynous males hunted more intensively on exposed sites and may have been exposed to greater predatory risks and energetic costs. The significant difference in time, and probably energy, spent by polygynous males in seeking and handling prey seemed to be at the expense of their personal upkeep, i.e., they spent less time preening or in other maintenance upkeep behavior (Table 1).

Acknowledgments.—We thank N. Lansky, A. Bashkin, and O. Rosa of the High School of Environmental Studies for helping in field observations, Y. Lubin and O. Hasson for commenting on the manuscript, and R. Conner and an anonymous referee for their constructive criticism. Work was supported by a Frank M. Chapman Award of the American Museum of Natural History and a grant from the Interuniversity Fund for Ecological Studies, Israel, to RY. This paper is contribution 110 of the Mitranti Center for Desert Ecology.

LITERATURE CITED

ALATALO, R. V., L. GUSTAFSSON, AND A. LUNDBERG. 1986. Do females prefer older males in polygynous bird species. Am. Nat. 127:241–245.

DANIN, A., G. ORSHAN, AND M. ZOHARY. 1975. The vegetation of the northern Negev and the Judean desert of Israel. Israel J. Bot. 24:118–172.

ORIANS, G. H. 1969. On the evolution of mating systems in birds and mammals. Am. Nat. 103:589–603.

REID, M. L. AND S. G. SEALY. 1986. Behavior of a polygynous yearling Yellow Warbler. Wilson Bull. 98:315–317.

SLAGSVOLD, T. 1986. Nest site settlement by the pied flycatcher: does the female choose her mate for the quality of his house or himself? Ornis Scand. 17:210–220.

STEELE, R. G. D. AND J. H. TORRIE. 1980. Principles and procedures of statistics. 2nd ed. McGraw Hill, New York.

TRIVERS, R. L. 1972. Parental investment and sexual selection. Pp. 136–179 *in* Sexual selection and the descent of man, 1871–1971 (B. Campbell, ed.). Aldine, Chicago, Illinois.

WITTENBERGER, J. F. 1981. Animal social behavior. Duxbury, Boston.

YOSEF, R. AND B. PINSHOW. 1988a. Nestling transfer in the Northern Shrike, in Israel. Auk 105:580–581.

——— AND ———. 1988b. Polygyny in the Northern Shrike (*Lanius excubitor*), in Israel. Auk 105:581–582.

REUVEN YOSEF, WILLIAM A. MITCHELL, AND BERRY PINSHOW, *Mitrani Center for Desert Ecology at the Jacob Blaustein Institute for Desert Research and Dept. of Biology, Ben-Gurion Univ., Sede Boqer Campus, 84993 Israel.* (Present address RY: *Dept. of Zoology, Ohio State Univ., Columbus, Ohio 43210; WAM: Dept. of Ecology and Evolutionary Biology, Univ. of Arizona, Tucson, Arizona 85721.*) *Received 7 June 1990, accepted 12 Sept. 1990.*