

- Pp. 95–131 in *Acoustic communication in birds*, vol. 1 (D. E. Kroodsma and E. H. Miller, Eds.). New York, Academic Press.
- DOOLING, R. J., T. J. PARK, D. D. BROWN, K. OKANOYA, & S. D. SOLI. 1987. Perceptual organization of acoustic stimuli by Budgerigars (*Melopsittacus undulatus*): II. vocal signals. *J. Comp. Psychol.* 101: 367–381.
- FALLS, J. B., A. G. HORN, & T. E. DICKINSON. 1988. How Western Meadowlarks classify their songs: evidence from song matching. *Anim. Behav.* 36: 579–585.
- LAMBRECHTS, M., & A. A. DHONDT. 1986. Male quality, reproduction, and survival in the Great Tit (*Parus major*). *Behav. Ecol. Sociobiol.* 19: 57–63.
- MCGREGOR, P. K., & J. R. KREBS. 1982. Song types in a population of Great Tits (*Parus major*): their distribution, abundance, and acquisition by individuals. *Behaviour* 79: 126–152.
- NELSON, D. A. 1988. Feature weighting in species song recognition by the Field Sparrow (*Spizella pusilla*). *Behaviour* 106: 158–182.
- SAS INSTITUTE INC. 1986. *SAS user's guide: statistics*, 1986 ed. Cary, North Carolina, SAS Inst. Inc.
- SHY, E., P. K. MCGREGOR, & J. R. KREBS. 1986. Discrimination of song types by male Great Tits. *Behav. Proc.* 13: 1–12.
- SOKAL, R. R., & F. J. ROHLF. 1969. *Biometry*. San Francisco, W. H. Freeman & Co.
- WEARY, D. M. 1989. Categorical perception of bird song: How do Great Tits (*Parus major*) perceive temporal variation in their song? *J. Comp. Psychol.* 103: 320–325.
- . 1990. Categorization of song notes by Great Tits: Which acoustic features are used and why? *Anim. Behav.* 39: 450–457.
- , J. R. KREBS, R. EDDYSHAW, P. K. MCGREGOR, & A. HORN. 1988. Decline in song output by Great Tits: exhaustion or motivation? *Anim. Behav.* 36: 1242–1244.

Received 24 April 1990, accepted 5 August 1990.

## Identification of Nest Predators by Photography, Dummy Eggs, and Adhesive Tape

RICHARD E. MAJOR<sup>1</sup>

*Department of Botany and Zoology, Monash University, Clayton, Victoria 3168, Australia*

Predation of the eggs and nestlings of birds (nest predation) is thought to be the prime cause of nest failure in most species (Lack 1954, Nice 1957, Skutch 1966, Ricklefs 1969, Best 1978, Best and Stauffer 1980, Nilsson 1986), but the culprit is rarely recorded. Predation is rarely observed because acts of predation are distributed over a long period of time and occur quickly (Skutch 1966, Best 1974). The vast majority of these observations have been restricted to daylight hours and may also be unreliable because the presence of an observer may discourage or attract certain predators (Bart 1977, Lenington 1979, Westmoreland and Best 1985, Major 1990). Inference of predator identity from the presence of potential predators is neither conclusive nor relevant to the relative importance of different predators. Monitoring predator movements near nests (Moors 1978, Clarke 1988) and recording parental reaction to nearby predators (Clarke 1988, Maher 1988) refine the assessment, but the reliability of the latter may be complicated by similar reactions to nonpredators and by habituation to genuine predators (McNicholl 1973).

Traditionally, ornithologists have relied on signs left at nests to determine the identity of predators. Predation by mustelids (Flack and Lloyd 1978 cited in

Moors 1983) and snakes (Skutch 1966, Best 1978, Best and Stauffer 1980) is said to be "clean," with no signs left at the nest (but for mink, see McNicholl 1982) except sometimes a hole in its center (Best 1978). Damage to the nest and flattening of the nest surroundings is associated with large mammals such as cats and foxes (Best 1978, Best and Stauffer 1980, Westmoreland and Best 1985). Rats and mice are said to leave fragments of shell or nestling in or under the nest (Rowley 1965; Best 1978; Moors 1978, 1983). The literature is unclear on the signs left by predatory birds. Some authors reported that nests remain intact (Gottfried and Thompson 1978, Best and Stauffer 1980); others found nests torn to pieces (e.g. Skutch 1966). This may vary with the type of predator or the type of nest. Maher (1988) suspected that the domed nests of Brown-backed Honeyeaters (*Ramsayornis modestus*) were torn apart by corvids, whereas Westmoreland and Best (1985) believed that corvids removed eggs from the open nests of Mourning Doves (*Zenaidura macroura*) and left the nest intact. Generalizations regarding signs at nests have been based on relatively few observations, although trials on animals held in captivity have increased sample size (Moors 1978). A further problem is that parents may remove nest materials from failed nests, which gives the appearance of nest damage by a predator (Skutch 1966, Marchant 1973). Parents might also remove their own eggs before nest desertion.

Predator identity is crucial for the management of

<sup>1</sup> Present address: Division of Environmental Science, The Australian Museum, 6–8 College Street, Sydney, New South Wales 2000, Australia.

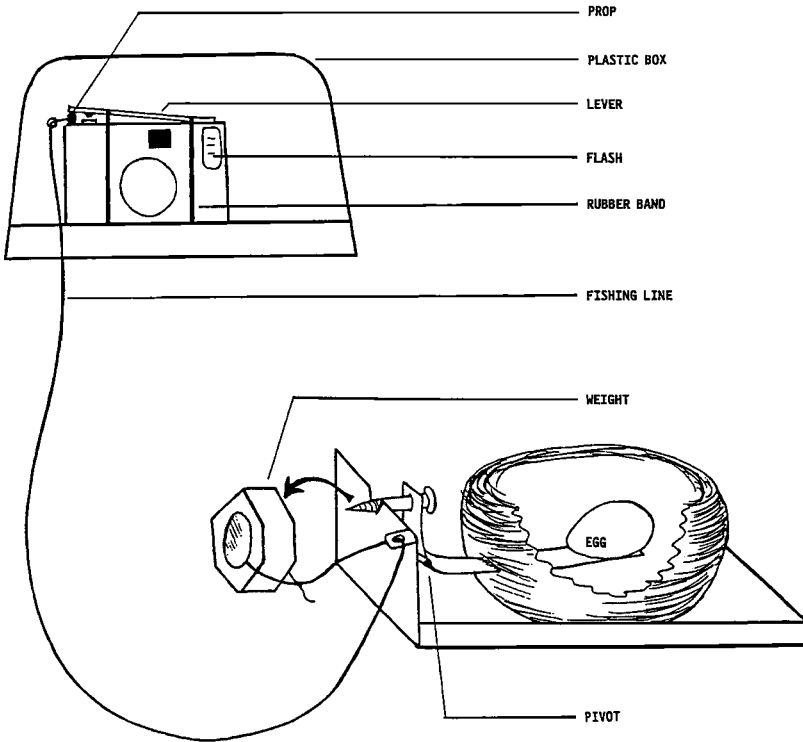


Fig. 1. Diagram of triggering mechanism used for remote photography. Movement of the egg caused a weight to drop. This pulled a line which removed a prop from a spring-loaded lever attached to the camera. Release of the lever depressed the shutter button. Only one exposure could be taken at any one time as the camera required manual resetting.

some endangered populations. Since human habitation, populations of many island species have declined, probably through destruction of habitat and the introduction of predators (King 1984). On Norfolk Island, Australia, I worked on Scarlet Robins (*Petroica m. multicolor*), which have declined since the 1960s. Nesting success of Scarlet Robins measured in 1987 was approximately 35% (Robinson 1988). All instances of predation were "clean," and because Norfolk Island is devoid of snakes and mustelids, avian predators were implicated. One possible avian predator of eggs and nestlings, the Boobook Owl (*Ninox novaeseelandiae*), was too rare to account for the intensity of predation. Others (the Nankeen Kestrel, *Falco cenchroides*; the Sacred Kingfisher, *Halcyon sancta*; and the White Tern, *Gygis alba*) did not enter the understory where robins nest. Potential mammalian predators included cats (*Felis catus*) and ship rats (*Rattus rattus*) introduced by Europeans some time since 1778, and the kiore (*Rattus exulans*) introduced by Polynesians much earlier. All three mammalian species were abundant in the understory, but no signs consistent with their predation were observed. To make management recommendations for Scarlet Robins on Nor-

folk Island, I obtained quantitative data on the identity of nest predators.

Fieldwork took place in the Norfolk Island National Park between October and December, 1988. For a description of the study site see ANPWS (1984). To keep human disturbance to a minimum, I used "artificial" nests of disused, cup-shaped, grass nests of White-fronted Chats (*Ephthianura albifrons*) rather than active Scarlet Robin nests. I mounted nests in trees in locations similar to those of active Scarlet Robin nests (2.5 m above the ground) and stocked them with eggs from captive Budgerigars (*Melopsittacus undulatus*), whose eggs are of similar size to eggs of Scarlet Robins. I used three methods to monitor predator activity in two separate experiments: (1) remote photography (see also Hussell 1974, Picman 1987, Savidge and Seibert 1988), (2) artificial eggs in which an identifiable imprint is left when a predator attempts to remove them (see also Moller 1987, 1989, 1990), and (3) double-sided tape positioned at nests to collect hairs or feathers of nest predators (see also Suckling 1978). Whenever predation occurred, the signs left at nests were recorded.

*Photography.*—Two cameras (Canon Snappies) with

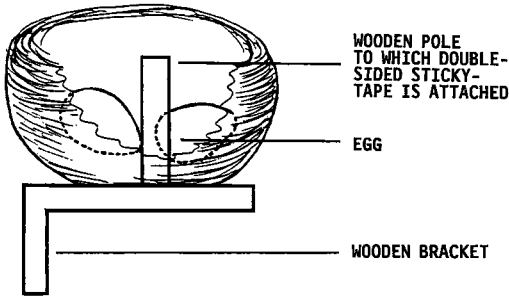


Fig. 2. Nest used for detection of predators by hairs left on double-sided sticky tape. The wooden bracket on the bottom is for attachment of the nest to a tree.

built-in flashes were mounted on trees 80 cm from "artificial" nests (one disused White-fronted Chat nest, one disused Scarlet Robin nest) that contained the triggering mechanism (Fig. 1). Cameras were set for a total of 94 camera days. Initially cameras were placed randomly, but as predation had not occurred at the first location after 15 days, the apparatus was taken to locations where predators were active (see below). After a nest was attacked, it was usually restocked with eggs for up to three photographs on subsequent nights, after which it was moved to a new location. Budgerigar eggs were used for 21 baitings, and nestlings of Eurasian Blackbird (*Turdus merula*) and European Starling (*Sturnus vulgaris*) were used for 8 baitings. Nestlings were fresh-frozen and used for only one night and only in nests in which eggs had been preyed on the previous day.

*Modeling clay and sticky tape.*—At each of six sites, 10 nests were erected in trees 10 m apart. One Budgerigar egg and one egg-shaped piece of white modeling clay were placed in five randomly chosen nests at each site. The other five nests contained two Budgeri-

TABLE 1. Results of 29 predation events on eggs and nestlings from artificial nests monitored with cameras (82 camera days for eggs and 12 for nestlings). The number of nests at which predators were photographed successfully is in parentheses.

	Number of nests	
	Eggs	Nestlings
No remains	9 (6)	8 (2)
Remains present		
In nest	2 (2)	0 (0)
Under nest	3 (1)	0 (0)
In and under	1 (1)	0 (0)
Remains not recorded <sup>a</sup>	6 (5)	0 (0)
Total	21 (15)	8 (2)

<sup>a</sup> For one predation event, a photograph was taken, but the eggs were not removed.

TABLE 2. Occurrence of predation of eggs at 60 artificial nests monitored by imprints left on "eggs" made of modeling clay or by hairs left on sticky-tape. All nests were inspected after 7 days. The number of nests at which predators were identified is in parentheses.

	Number of nests	
	Sticky-tape	Model. clay
No remains	8 (1)	12 (5)
Remains present		
In nest	5 (0)	4 (4)
Under nest	7 (2)	4 (3)
In and under	4 (0)	4 (4)
Survived	6	6
Total	30 (3)	30 (16)

gar eggs and a central vertical pole covered with double-sided sticky-tape (Fig. 2). All nests were checked seven days later.

I obtained photographs of 15 cases of egg predation and 2 of nestling predation at seven different locations (Table 1). Another six nests with eggs and six with young were preyed on, but the photographs failed to show the predator. In each identified case, *Rattus rattus* was responsible, judging from the tail length (Fig. 3 upper. B) and body size (Phil Moors pers. comm.).

Eggs made of modeling clay always carried imprints when nests were preyed on (Table 2), although the extent was variable (Fig. 3 lower). Some eggs had only a few tooth imprints, some were chewed extensively, some were chewed into numerous pieces, and others were removed completely. In every case tooth marks were those of rats, but the species could not be identified.

Heavy rain in the 24 h subsequent to setup removed the adhesive from most of the nests with sticky-tape so that hair was collected at only three nests (Table 2). Only one hair sample could be analyzed, and it most likely belonged to *Rattus exulens* (Barbara Triggs in litt.).

In 69 experimental nests with eggs that were preyed on, the predator was identified in 34 cases (49%). No predators other than rats were detected, but fragments of eggshell were absent from 41% of identified egg predation and a comparable percentage of all predation attempts. There were eight incidents of predation of nestlings during which all nests were left clean. The predator appeared in only two of these photographs, and it was *Rattus rattus* on both occasions.

Every attributable case of nest predation was due to rats, probably *Rattus rattus*. However, if I assumed that rats always leave shells at nests, I would have underestimated rat predation by approximately 40%, as remains were present in only 59% of cases. Rats

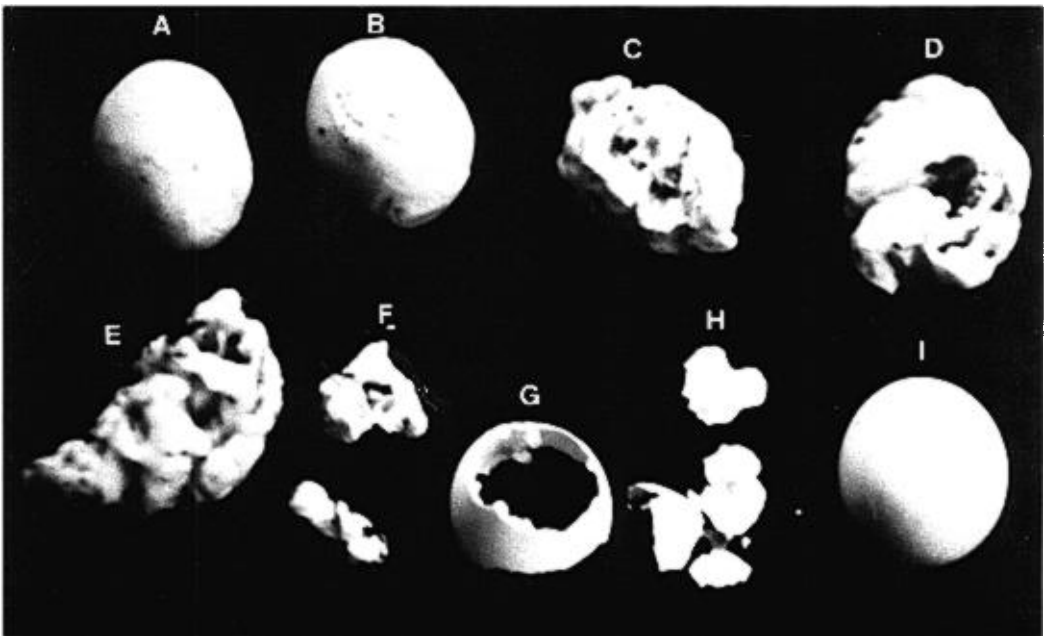
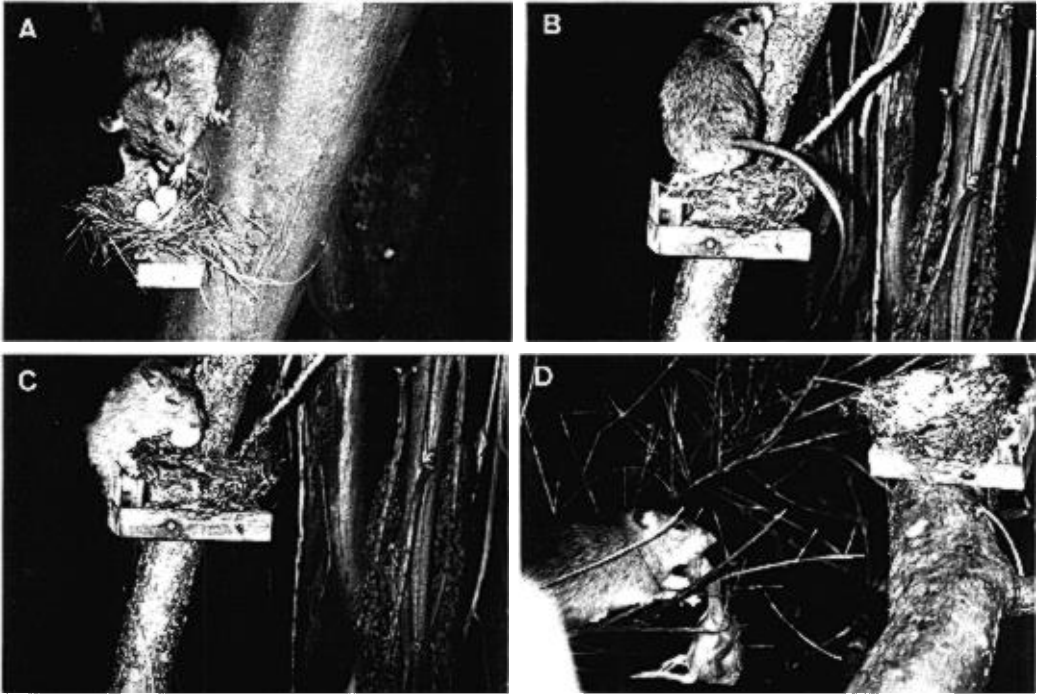


Fig. 3. Upper: Photographs (A-D) of predators at artificial nests taken by a camera triggered automatically (Mag.  $\times 0.2$ ). The large size of the rats indicates that they are all *Rattus rattus*. Lower: Remains of "eggs" made of modeling clay (A-F) and Budgerigar eggs (G-I) after varying degrees of interference by rats (Mag.  $\times 1.3$ ). Untouched modeling clay shown in A; untouched egg shown in I.

evidently sometimes carried eggs from nests before attempting to eat them (Fig. 3 upper: C). Egg remains were once found on a log 5 m from a nest, and eggshells have been found in rat nests (Charli Mizzi pers. comm.). Rats also carried nestlings from the nest (Fig. 3 upper: D). Individual variation in feeding behavior of rats may be affected by numerous factors including the clutch size and the sex of the rat. It is possible that when confronted with several eggs a rat is more likely to eat one at the nest before removing others. Perhaps rats with dependent young are more likely to carry food back to their nests. These results do not confirm previous observations of nest predation by captive *Rattus rattus* for which shells were left at all nests (Moors 1978). In the confined space of a cage there is less option for rats to carry eggs away from the nest, and it is possible that eggs of different species receive different treatment.

Nests containing eggshell fragments consistent with "traditional" rat predation were found at two nests of Eurasian Blackbird, and one of Grey Gerygone (*Gerygone igata*). However, in contrast to experimental nests containing eggs, at which shell fragments were left at 59% of nests, no signs were left at any active Scarlet Robin nests. Presumably, this was because at least 5 of the 7 losses were of nestlings, and nestling predation was shown (by experimental nests) to be clean. Because most losses occurred during the nestling stage, most predation would therefore go undetected.

The time of day of nest predation could not be determined directly for nests containing sticky-tape or modeling clay, but the background of all photographs was black, indicating predation took place at night. Most nest observation occurs during the day, and it is unlikely that identification of predators could have been made by traditional observation methods even though the predation rate was extremely high.

Over this period, predation of artificial nests was much higher than predation of active Scarlet Robin nests. I used the Mayfield method (Mayfield 1961, 1975; Johnson 1979) to measure nesting success of Scarlet Robins in 1988. Sample size was small (22 nests), but nesting success appeared to be low (31%; 95% confidence limits between 14% and 67%). There were four likely causes for the difference in predation rate of active and artificial nests. (1) Predators may have been more abundant in the experimental areas than in the area of the forest where most Scarlet Robin nests were observed. (2) Artificial nests may have been positioned too close together, and a few rats may have accounted for most of the losses. (3) I may have used some bad eggs, and olfaction may have enhanced nest-finding. (4) Artificially placed nests may have been more visible or may have carried human signs attractive to predators. Additional experiments in the area where most Scarlet Robin nests were found yielded lower predation (8 of 64 nests). Further, 3 of the 8 nests that were preyed on contained modeling

clay only, which indicates that smelly eggs were unlikely to have caused the different predation rate. Another experiment in one of the original areas, but with 25 m between nests instead of the initial 10 m, yielded predation intensity (7 of 10 nests) similar to the first trial. I believe that nest-spacing was unimportant over this range and that rat abundance varied between localities.

Like previous studies that used cameras (Hussell 1974; Picman 1987, 1988; Savidge and Seibert 1988), artificial eggs (Moller 1987, 1989, 1990), hair-catchers (Yahner and Wright 1985), and tracking paper (Moors 1978, Wilcove 1985), I showed that manipulative methods can be used to identify nest predators. Like the work of Savidge and Seibert (1988), these techniques provide specific data on the signs left by predators, but because of variation in individual behavior, identification of predators according to sign must be made with caution. Manipulative methods also have problems. Artificial eggs may not accurately simulate genuine eggs, hairs or tracks may often be missed (Wilcove 1985, Yahner and Wright 1985), and the apparatus used for these methods and photography may attract or repel some predators (Yahner and Wright 1985). A combination of methods is therefore desirable. The study was limited because all data were recorded from artificial nests that may conceivably attract different predators than nests attended by parent birds (Loiselle and Hoppes 1983, Martin 1987). Comparison of predation at artificial and real nests is urgently required as artificial nests are popular tools for studies of avian nest predation.

This work was undertaken as part of a consultancy agreement with the Australian National Parks and Wildlife Service. I am grateful to John Hicks, Margaret Christian, Mark Hallam, and Derek Greenwood for their help. I am indebted to Doug Robinson, who introduced me to Scarlet Robins, started the project, and offered his suggestions at all times. The following Norfolk Islanders provided invaluable local knowledge: Margaret Christian, Ken Christian, Beryl Evans, Owen Evans, Arthur Evans, Lyn Evans, and Honey McCoy. Phil Moors helped with identification of photographs of rats, and Barbara Triggs identified the hair sample. John Buchan and Charli Mizzi supplied me with eggs; Steve Morton provided ideas and advice on remote photography; and Mike Cullen, Doug Robinson, Kris French, Kathy Winnet-Murray, Martin McNicholl, and Alan H. Brush provided valuable criticism of the text. To all of them I am grateful.

#### LITERATURE CITED

- AUSTRALIAN NATIONAL PARKS AND WILDLIFE SERVICE. 1984. Plan of management for Norfolk Island National Park and Norfolk Island Botanical Garden. Canberra, Commonwealth of Australia.
- BART, J. 1977. Impact of human visitations on avian nesting success. *Living Bird* 16: 187-192.

- BEST, L. B. 1974. Blue racers prey on Field Sparrow nests. *Auk* 91: 168-169.
- . 1978. Field Sparrow reproductive success and nesting ecology. *Auk* 95: 9-22.
- , & D. F. STAUFFER. 1980. Factors affecting nesting success in riparian bird communities. *Condor* 82: 149-158.
- CLARKE, M. F. 1988. The reproductive behaviour of the Bell Miner *Manorina melanophrys*. *Emu* 88: 88-100.
- FLACK, J. A. D., & B. D. LLOYD. 1978. The effect of rodents on the breeding success of the South Island robin. Pp. 59-66 in *The ecology and control of rodents in New Zealand Nature Reserves*, vol. 4 (P. R. Dingwall, I. A. E. Atkinson, and C. Hay, Eds.). Wellington, Dep. Lands Surv. Inf. Ser.
- GOTTFRIED, B. M., & C. F. THOMPSON. 1978. Experimental analysis of nest predation in an old-field habitat. *Auk* 95: 304-312.
- HUSSELL, D. T. J. 1974. Photographic records of predation at Lapland Longspur and Snow Bunting nests. *Can. Field-Nat.* 88: 503-506.
- JOHNSON, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96: 651-661.
- KING, C. 1984. Immigrant killers. Introduced predators and the conservation of birds in New Zealand. Auckland, Oxford Univ. Press.
- LACK, D. 1954. *The natural regulation of animal numbers*. Oxford, Clarendon Press.
- LENINGTON, S. 1979. Predators and blackbirds: the "uncertainty principle" in field biology. *Auk* 96: 190-192.
- LOISELLE, B. A., & W. G. HOPPES. 1983. Nest predation in insular and mainland lowland rainforest in Panama. *Condor* 85: 93-95.
- MAHER, W. J. 1988. Breeding biology of the Brown-backed Honeyeater *Ramsayornis modestus* (Meliphagidae) in northern Queensland. *Emu* 88: 190-194.
- MAJOR, R. E. 1990. The effect of human observers on the intensity of nest predation. *Ibis* 132: 608-612.
- MARCHANT, S. 1973. Analysis of nest-records of the Willie Wagtail. *Emu* 74: 149-160.
- MARTIN, T. E. 1987. Artificial nest experiments: effects of nest appearance and type of predator. *Condor* 89: 925-928.
- MAYFIELD, H. F. 1961. Nesting success calculated from exposure. *Wilson Bull.* 73: 255-261.
- . 1975. Suggestions for calculating nest success. *Wilson Bull.* 87: 456-466.
- McNICHOLL, M. K. 1973. Habituation of aggressive responses to avian predators by terns. *Auk* 90: 902-904.
- . 1982. Factors affecting reproductive success of Forster's Terns at Delta Marsh, Manitoba, Colon. *Waterbirds* 5: 32-38.
- MOLLER, A. P. 1987. Egg predation as a selective factor for nest design: an experiment. *Oikos* 50: 91-94.
- . 1989. Nest site selection across field-woodland ecotones: the effect of nest predation. *Oikos* 56: 240-246.
- . 1990. Nest predation selects for small nest size in the blackbird. *Oikos* 57: 237-240.
- MOORS, P. J. 1978. Methods for studying predators and their effects on forest birds. Pp. 47-57 in *The ecology and control of rodents in New Zealand Nature Reserves*, vol. 4 (P. R. Dingwall, I. A. E. Atkinson, and C. Hay, Eds.). Wellington, Dep. Lands Surv. Inf. Ser.
- . 1983. Predation by mustelids and rodents on the eggs and chicks of native and introduced birds in Kowhai Bush, New Zealand. *Ibis* 125: 137-154.
- NICE, M. M. 1957. Nesting in altricial birds. *Auk* 74: 305-321.
- NILSSON, S. G. 1986. Evolution of hole-nesting in birds: on balancing selection pressures. *Auk* 103: 432-435.
- PICMAN, J. 1987. An inexpensive camera set-up for the study of egg predation at artificial nests. *J. Field Ornithol.* 58: 372-382.
- . 1988. Experimental study of predation on eggs of ground-nesting birds: effects of habitat and nest distribution. *Condor* 90: 124-131.
- RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contrib. Zool.* 9: 1-48.
- ROBINSON, D. 1988. Ecology and management of the Scarlet Robin, White-breasted White-eye and Long-billed White-eye on Norfolk Island. Melbourne, ANPWS rep.
- ROWLEY, I. R. 1965. The life history of the Superb Blue Wren *Malurus cyaneus*. *Emu* 64: 251-297.
- SAVIDGE, J. A., & T. F. SEIBERT. 1988. An infrared trigger and camera to identify predators at artificial nests. *J. Wildl. Manage.* 52: 291-294.
- SKUTCH, A. F. 1966. A breeding bird census and nesting success in central America. *Ibis* 108: 1-16.
- SUCKLING, C. C. 1978. A hair sampling tube for the detection of small mammals in trees. *Australian Wildl. Res.* 5: 249-252.
- WESTMORELAND, D., & L. B. BEST. 1985. The effect of disturbance on Mourning Dove nesting success. *Auk* 102: 774-780.
- WILCOVE, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66: 1211-1214.
- YAHNER, R. H., & A. L. WRIGHT. 1985. Depredation on artificial ground nests: effects of edge and plot age. *J. Wildl. Manage.* 49: 508-513.

Received 20 February 1990, accepted 5 August 1990.