J Raptor Res. 28(3):143–148

FACTS AND ARTEFACTS IN NEST-BOX STUDIES: IMPLICATIONS FOR STUDIES OF BIRDS OF PREY

ANDERS PAPE MØLLER
Department of Zoology, Uppsala University, Villavägen 9, S-752 36 Uppsala, Sweden

ABSTRACT.—Biologists study free-living organisms in order to determine the extent to which they are adapted to their environment (which includes abiotic factors, conspecifics and heterospecifics). Ornithologists have exploited the fact that a number of hole-nesting birds readily breed in nest boxes. Boxes are artificial environments which often reduce the negative effects of nest predation and ectoparasitism, and nest boxes are frequently provided at unnaturally high densities. These aspects of nest-box studies may have important implications for the interpretation of current knowledge of the life history, population dynamics, and ecology of birds because much of the information is derived from nest-box studies. I review the consequences of nest-box studies for the inferences which can be made on bird biology in general and raptor biology in particular. Finally, I suggest ways in which the results obtained from nest boxes can be generalized by quantifying the bias of nest-box studies as compared to studies of the same species breeding in natural cavities.

KEY WORDS: *experimental validity*; *natural cavities*; *nest boxes*; *nest predation*; *parasitism*.

Realidades y artefactos en estudios de cajas anideras: implicaciones para el estudio de aves de presa

RESUMEN.—Estudios biológicos de organismos silvestres se realizan para determinar la extensión a la que ellos están adaptados al medio ambiente (que incluye factores abióticos, conespecíficos y heteroespecíficos). Los ornitólogos han explotado el hecho de que un gran número de aves que nidifican en cuevas o galerías, se reproducen en cajas anideras. Las cajas son medios ambientes artificiales que a menudo reducen el efecto negativo de la depredación y el ectoparasitismo, además están disponibles en altas densidades, que no necesariamente son naturales. Estos aspectos del estudio de cajas anideras, puede tener importantes implicaciones en la interpretación de conocimientos sobre la historia de vida, dinámica poblacional y ecología de las aves, porque mucha de la información ha sido derivada precisamente de estudios de este tipo. Revisé las consecuencias del estudio de cajas anideras respecto a las inferencias que podrían ser hechas sobre la biología de aves en general y sobre la biología de rapaces en particular. Finalmente, sugiero maneras en las que los resultados obtenidos de estos estudios podrían ser generalizados, cuantificando el error que se obtiene al comparar con estudios de la misma especie que se reproducen en cavidaes naturales.

[Traducción de Ivan Lazo]

Current knowledge of the biology of birds is vast compared to that of many other classes of organisms, and this is mainly due to the immense interest in birds and the ease with which bird studies are performed. A large amount of information on avian biology can be attributed to the success of nest-box studies, and areas of research influenced by these studies include population regulation, life history evolution, quantitative genetics, sexual selection, and reproductive physiology. Many of the results have been included in textbooks and form the basis for generalizations on bird biology.

Ornithologists put up nest boxes for the joy and pleasure of having breeding birds around, the wish to enhance population size and reproductive success of cavity-nesting birds, and the ease at which biological studies can be performed on birds in nest boxes. If the objective of using nest boxes is the second, or particularly the third, mentioned above, there are reasons to plan the study carefully, because nest boxes differ from natural cavities in a number of different ways, and this affects predation risks and infestations with parasites, and therefore potentially a number of reproductive parameters (Møller 1989, 1992). Most individuals of cavity-nesting species breed in natural holes and it is likely that they are adapted to this environment. Individuals breeding in nest boxes mainly originate from the fraction of the population breeding in natural cavities, and this may make tests of adaptive hypotheses difficult by relying entirely on populations breeding in nest boxes.

I briefly review (1) the effect of nest boxes on the probability of nest predation and ectoparasite infestations, (2) the effect of nest-box density on reproduction and interspecific relationships, and (3) the relationship between features of nest-box design and avian reproduction. This is done by relying extensively on the vast literature on hole-nesting birds including that on raptors.

COMPARISON OF NEST BOXES AND NATURAL CAVITIES

Nest Predation. Nest predation is one of the most important determinants of the reproductive success of birds (Ricklefs 1969). Cavity-nesting birds have been supposed to suffer less often than open-nesting species (Lack 1954, Nice 1957, Ricklefs 1969, Korpimäki 1984, Sonerud 1985), but this apparent difference is due to low nest-predation estimates obtained from nest-box studies. A Swedish study of seven different cavity-nesting passerine birds revealed on average 62% lower mortality due to predation in boxes as compared to natural cavities (Nilsson 1984), and similar results have been obtained elsewhere (Korpimäki 1984, Lundberg and Alatalo 1992). Unbiased estimates of nest predation on hole-nesting birds breeding in natural cavities do not suggest that the predation rate is any lower than in open-nesting species breeding under similar environmental conditions (Nilsson 1986).

Nest predation rates may depend on the intensity of begging calls of offspring as mediated by their hunger level (Skutch 1976). Offspring raised under poor environmental conditions (in poor habitats, outside the main breeding season, or by parents of low phenotypic quality) may suffer from predation more often than others. The use of nest boxes and the resultant reduction in nest predation is therefore likely to particularly improve the reproductive success of individuals of poor phenotypic quality (e.g., young birds from poor habitats of low competitive ability).

Nest predation may be relatively less important for birds of prey breeding in nest boxes, because these species are able to efficiently defend the box against predators. However, mammalian predators are sometimes important in boxes inhabited by owls (Sonerud 1985). The extent to which nest-predation rates of birds of prey differs between boxes and natural cavities has not been quantified (but see Korpimäki (1984) for a preliminary study).

The effective elimination of nest predation from boxes may affect nest site choice of females (Alatalo et al. 1986) and increase the overall reproductive success of birds, particularly of individuals of low phenotypic quality. Reproductive strategies of birds have been suggested to be influenced by nest predation (e.g., Slagsvold 1982, Lundberg 1985, Lima 1987), and the reproduction of birds breeding in predator-safe boxes may be severely affected by the absence of any predation risk. Tawny owls (*Strix aluco*) at some locations in Britain prefer nest boxes and have abandoned natural sites entirely (Petty et al. 1994).

Ectoparasitism. Ectoparasitism may play an important role in the life of birds, and affects aspects as diverse as reproduction, interspecific interactions, and sexual selection (Price 1980, Price et al. 1988, Hamilton and Zuk 1982, Loye and Zuk 1991). Ectoparasites are common inhabitants of cavity nests, and a number of experimental studies have demonstrated severe negative effects on reproductive performance (review in Møller et al. 1990). The high virulence of ectoparasites of hole-nesting birds may be due to their frequent horizontal transmission to other conspecific host individuals. Horizontal transmission is likely to increase the virulence of parasites while vertical transmission generally selects for reduced virulence (Ewald 1980). Old nests and their contents have traditionally been removed from nest boxes, even though this procedure has not been reported in publications (Møller 1989, 1992). Scientists using nest boxes as a tool have repeatedly explained to me, when asked why they removed old nests from their boxes, that nest removal was adopted because ectoparasites were a nuisance to birds and field assistants! Nest removal may have resulted in substantial reductions in ectoparasite loads of nest boxes compared to that of natural cavities.

Ectoparasites have a number of detrimental effects on bird hosts. These effects include reduced attractiveness of potential nest sites, delayed reproduction, increased mortality, reduced growth rate, premature fledging, and reduced future reproductive potential (e.g., Moss and Camin 1970, Brown and Brown 1986, Møller 1993). Ectoparasites are frequent vectors of diseases (e.g., Price 1980, Marshall 1981), and reductions in ectoparasite loads may reduce the probability of disease transmission.

The effects of parasite abundance on reproductive performance have been assessed experimentally in a number of bird species. One interesting finding is that the same ectoparasite species may have dramatically different virulence in different populations of the same host species (Richner et al. 1994a, 1994b, K. Allander and R. Dufva unpubl. data). This result suggests that it is difficult to make any generalizations from one study to another, even when the same host and parasite is involved.

There is no information available on differences between boxes and natural cavities for raptor ectoparasite infestations, but the removal of debris and, hence, parasites from nest boxes may reduce the variance in reproductive success of hosts, particularly due to improved reproductive performance of host individuals of poor phenotypic quality (Møller et al. 1993). Raptors may also suffer from horizontal transmission of virulent parasites from prey, particularly in natural nest sites where prey remains are left behind.

Population Density. This feature has been hypothesized to affect a number of reproductive variables such as the timing of reproduction, clutch size, and reproductive failure (Lack 1954, 1966). The direct effect of population density has only been verified experimentally in a few cases (Lundberg and Alatalo 1992), although the amount of circumstantial evidence is considerable. Most nest-box studies are characterized by higher population densities than in surrounding areas without boxes (e.g., Marti et al. 1979, Ziesemer 1980). Population density is known to affect the intensity of both intraspecific and interspecific interactions (e.g., Lundberg and Alatalo 1992). Density-dependent intraspecific competition may account for some of the reductions in reproductive success at high densities, but this effect will depend on whether birds breed in natural cavities or boxes. Provisioning of boxes has been shown to result in dramatic increases of local population density of birds (von Haartman 1971) including raptors (Marti et al. 1979), perhaps severely increasing the intensity of intraspecific competition. Density-dependent nest predation has been reported from one study of nest-box breeding tits (Dunn 1977). The intensity and the prevalence of ectoparasitism are density-dependent in a number of cases (review in Møller et al. 1993). Ectoparasites particularly have detrimental effects on their hosts during poor environmental conditions (Møller et al. 1993); for example, at high population densities. The reproductive success of hosts breeding in nest boxes may therefore particularly be improved at high population densities when hosts otherwise are severely negatively affected by parasitism.

The negative effects of nest predation, ectoparasitism, and population density may interact synergistically in a number of different ways. The effects of interspecific interactions may be particularly severe under high population densities, because resource abundance per individual is low. The effects of nest predation may also be aggravated under high levels of ectoparasitism, because parasite infestation may increase the level of hunger and the begging intensity of offspring. Interaction effects on reproduction are likely to be reduced in nest-box studies, where the level of parasitism and the risk of nest predation are low.

Design of Nest Boxes. The size of cavities affects the frequency of occupation in a number of different bird species, including raptors (e.g., van Balen 1984, van Balen et al. 1982, Rendell and Robertson 1989, Bortolotti 1994). Cavity size and location affect predation risk (e.g., Lundberg and Alatalo 1992), and settlement by prospective breeders may therefore depend on the phenotypic quality of individuals. Low quality individuals may be unable to get access to preferred natural nest sites and be forced to accept nest boxes of lower quality. Alternatively, nest-box dimensions may exceed what is available in the environment, and a small number of nest boxes may result in primarily high quality individuals settling in boxes.

A second feature of some cavity-nesting species, including raptors, is that reproductive parameters appear to be adjusted to the size of the cavity (e.g., Karlsson and Nilsson 1977, van Balen 1984, Korpimäki 1985, Bortolotti 1994). One study has reported a causal relationship between cavity size and clutch size in tits (Löhrl 1973). It is also possible that birds may be able to assess the risk of nest predation as determined by the features of the nest cavity and adjust reproductive investment to perceived risks (see Sonerud (1985) for a case of nest site choice in Tengmalm's owl *Aegolius funereus*). The reproductive success of birds breeding in nest boxes can therefore directly be influenced by the size of boxes provided, and the features of nest boxes should preferably reflect what is available in natural cavities, if scientists intend to make inferences about the adaptive nature of reproductive decisions.

CONCLUSIONS

The points raised in this paper may appear to be of minor importance compared to the amount of information gained from large-scale population studies using boxes (Koenig et al. 1992). This conclusion is premature, because most current studies of cavity-nesting bird species address ecological and micro-evolutionary questions with the hidden assumption that birds are able to utilize the situation in nest boxes in the same way as natural sites. For example, scientists have for several decades studied optimal clutch size in hole-nesting birds by relying entirely on birds breeding in nest boxes, that exclude or reduce important causes of nest failure. However, the assumption of comparable responses in natural nest sites and in boxes has not been rigorously tested and this gives rise to a host of validity problems.

Experimental studies usually consider four different types of validity, viz. statistical conclusion validity, internal validity, construct validity, and external validity (e.g., Cochran and Cox 1957). There may not be a high degree of statistical conclusion validity in nest-box studies if there is no covariation between two or more variables of interest. The internal validity may also be low if there is a lack of standardization of treatments within and between subjects, as would be the case if a particular kind of bird such as competitively superior individuals are attracted to predator-safe nest boxes. There may also be problems with construct validity which relates to the cause and effect constructs involved in the relationship. For example, if the effect of population density on reproduction is studied in a nest-box experiment, there may be other differences between plots than differences in density; for example, if a larger proportion of low quality individuals breed in boxes provided at a high density. Finally, nest-box studies may suffer from problems with external validity, because it is impossible to generalize a probably causal relationship across individuals, times and settings (natural cavities and boxes). External validity may be reduced because of interactions between selection and treatment if a particular kind of individual is attracted at high population densities, because of interactions between settings and treatment (population density is higher in nest-box plots), and because of interactions between history and treatment (individuals that have previously bred in boxes may preferentially settle in high density plots).

RECOMMENDATIONS

The current knowledge of birds is to a large extent due to studies of hole-nesting species. Scientists have exploited the opportunity to obtain information on large numbers of individual birds throughout their lives by providing nest boxes. My criticism is not an attempt to discard previous knowledge but to encourage better nest-box studies in order to validate the results of previous studies. This can be done by following a number of simple recommendations.

First, it is very important that scientists report exactly what has been done in a particular study. Only detailed knowledge of what was done will allow comparison of results from studies in different sites. A brief list of questions includes the following: What was the size of boxes and the size of the entrance hole? Were new boxes provided annually? Were old nests or nest-box debris removed? What was the density of boxes?

Second, nest-box size and the size of entrance holes have been found to affect occupancy and various life history characters. This problem can be handled in two different ways. Nest boxes with mean dimensions resembling those of natural cavities occupied by the species can be provided. Alternatively, the experimenter may in a pilot study provide boxes of a range of different sizes and record the response of the species to variation in box size and the size of entrance holes.

Third, it is essential for all nest-box studies that comparisons are made between reproductive parameters in nest boxes and in natural cavities. This has now been done in a number of species (e.g., Korpimäki 1984, Robertson and Rendell 1990, Lundberg and Alatalo 1992, Bortolotti 1994, Gehlbach 1994), and many studies have reported increased mean and/or reduced variance in reproductive success in boxes. Assessment of reproduction in boxes versus natural cavities could preferentially be made in a pairwise design which controls for differences in environmental conditions (Gehlbach 1994). This will allow conclusions about the extent to which observations from boxes are comparable to those from natural cavities.

ACKNOWLEDGMENTS

F.R. Gehlbach kindly provided constructive criticism. I thank the Swedish Natural Science Research Council for support.

LITERATURE CITED

ALATALO, R.V., A. LUNDBERG AND C. GLYNN. 1986 Female pied flycatchers choose territory quality and not male characteristics. *Nature (Lond.)* 323:152–153.

BORTOLOTTI, G.R. 1994. Effects of nest-box size on nest-site preference and reproduction in American kestrels. *J. Raptor Res.* 28:127–133.

BROWN, C.R. AND M.B. BROWN. 1986. Ectoparasitism as a cost of coloniality in the cliff swallow (*Hirundo pyrrhonota*). *Ecology* 67:1206–1218.

COCHRAN, W.D. AND G.M. COX. 1957. Experimental design. Wiley, New York, NY U.S.A.

DUNN, E.K. 1977. Predation by weasels (*Mustela nivalis*) on breeding tits (*Parus* spp.) in relation to the density of tits and rodents. *J. Anim. Ecol.* 46:633–652.

EWALD, P.W. 1980. Evolutionary biology and the treatment of signs and symptoms of infectious disease. *J. Theor. Biol.* 86:169–176.

GEHLBACH, F.R. 1994. Nest-box versus natural-cavity nests of the eastern screech-owl: an exploratory study. *J. Raptor Res.* 28:154–157.

HAMILTON, W.D. AND M. ZUK. 1982. Heritable true fitness and bright birds: a role for parasites? *Science* 218:384–387.

KARLSSON, J. AND S.G. NILSSON. 1977. The influence of nest-box area on clutch size in some hole-nesting passerines. *Ibis* 129:243–258.

KOENIG, W.D., P.A. GOWATY AND J.L. DICKINSON. 1992. Boxes, barns, and bridges: confounding factors or exceptional opportunities in ecological studies. *Oikos* 63: 305–308.

KORPIMÄKI, E. 1984. Clutch size and breeding success of Tengmalm's owl *Aegolius funereus* in natural cavities and nest boxes. *Ornis Fenn.* 61:80–83.

———. 1985. Clutch size and breeding success in relation to nest-box size in Tengmalm's owl *Aegolius funereus*. *Holarct. Ecol.* 8:175–180.

LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford, U.K.

———. 1966. Population studies of birds. Clarendon Press, Oxford, U.K.

LIMA, S.L. 1987. Clutch size in birds: a predation perspective. *Ecology* 68:1062–1070.

LÖHRL, H. 1973. Einfluss der Brutraumfläche auf die Gelegegrösse der Kohlmeise. *J. Ornithol.* 114:339–347.

LOYE, J.E. AND M. ZUK [EDS.]. 1991. Bird-parasite interactions: ecology, evolution, and behaviour. Oxford Univ. Press, Oxford, U.K.

LUNDBERG, A. AND R.V. ALATALO. 1992. The pied flycatcher. T. & A.D. Poyser, London, U.K.

LUNDBERG, S. 1985. The importance of egg hatchability and nest predation on clutch size evolution in altricial birds. *Oikos* 45:110–117.

MARSHALL, A.G. 1981. The ecology of ectoparasitic insects. Academic Press, London, U.K.

MARTI, C.D., P.W. WAGNER AND K.W. DENNE. 1979. Nest boxes for the management of barn owls. *Wildl. Soc. Bull.* 7:145–148.

MØLLER, A.P. 1989. Parasites, predators and nest boxes: facts and artefacts in nest box studies of birds? *Oikos* 56:421–423.

———. 1992. Nest boxes and the scientific rigour of experimental studies. *Oikos* 63:309–311.

———. 1993. Ectoparasites increase the cost of reproduction in their hosts. *J. Anim. Ecol.* 62:309–322.

———, K. ALLANDER AND R. DUFVA. 1990. Fitness effects of parasites on passerine birds: a review. Pages 269–280 *in* J. Blondel, A. Gosler, J.D. Lebreton, and R. McCleery [EDS.], Population biology of passerine birds: an integrated approach. Springer-Verlag, Berlin, Germany.

———, R. DUFVA AND K. ALLANDER. 1993. Parasites and the evolution of host social behavior. *Adv. Study Behav.* 22:65–102.

MOSS, W.W. AND J.H. CAMIN. 1970. Nest parasitism, productivity, and clutch size in purple martin. *Science* 168:1000–1003.

NICE, M.M. 1957. Nesting success in altricial birds *Auk* 74:305–321.

NILSSON, S.G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. *Ornis Scand.* 15:167–175.

———. 1986. Evolution of hole-nesting in birds: on balancing selection pressures. *Auk* 103:432–435.

PETTY, S.J., G. SHAW AND D.I.K. ANDERSON. 1994. Value of nest boxes for population studies and conservation of owls in coniferous forests in Britain. *J Raptor Res.* 28:134–142.

PRICE, P.W. 1980. Evolutionary biology of parasites Princeton Univ. Press, Princeton, NJ U.S.A.

———, M. WESTOBY AND B. RICE. 1988. Parasite-mediated competition: some predictions and tests. *Am. Nat.* 131:544–555.

RENDELL, W.B. AND R.J. ROBERTSON. 1989. Nest-site characteristics, reproductive success and cavity availability for tree swallows breeding in natural cavities *Condor* 91:875–885.

RICHNER, H., A. OPPLINGER AND P. CHRISTE. 1994a Effect of an ectoparasite on reproduction in great tits *J. Anim. Ecol.* (in press).

———, P. CHRISTE AND A. OPPLINGER. 1994b. Ectoparasites affect timing of breeding in the great tit (*Parus major*). *Behav. Ecol.* (in press).

RICKLEFS, R.E. 1969. An analysis of nesting mortality in birds. *Smithson. Contrib. Zool.* 9:1–48.

ROBERTSON, R.J. AND W.B. RENDELL. 1990. A comparison of the breeding ecology of a secondary cavity-breeding bird, the tree swallow (*Tachycineta bicolor*) in nest-boxes and natural cavities. *Can. J. Zool.* 68:1046–1052.

SKUTCH, A.F. 1976. Parent birds and their young. Texas Univ. Press, Austin, TX U.S.A.

SLAGSVOLD, T. 1982. Clutch size variation in passerine birds: the nest predation hypothesis. *Oecologia* 54:159–169.

SONERUD, G. 1985. Nest-site shift in Tengmalm's owl *Aegolius funereus* as defense against predation involving long-term memory in the predator. *J. Anim. Ecol.* 54: 179–192.

VAN BALEN, J.H. 1984. The relationship between nest-box size, occupation and breeding parameters of the great tit *Parus major* and some other hole-nesting species. *Ardea* 72:163–175.

———, C.J.H. BOOY, J.A. VAN FRANEKER AND E.R. OSIECK. 1982. Studies on hole-nesting birds in natural nest sites. 1. Availability and occupation of natural nest sites. *Ardea* 70:1–24.

VON HAARTMAN, L. 1971. Population dynamics. Pages 391–459 *in* D.S. Farner and J.R. King [EDS.], Avian biology. Vol. 1. Academic Press, New York, NY U.S.A.

ZIESEMER, F. 1980. Siedlungsdichte und Bruterfolg von Schliereulen (*Tyto alba*) in einer Probefläche vor und nach dem Anbringen von Nisthilfen. *Vogelwelt* 101: 61–66.

Received 3 December 1993; accepted 18 July 1994