

Nest predation increases with parental activity: separating nest site and parental activity effects

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Alexander Skutch hypothesized that increased parental activity can increase the risk of nest predation. We tested this hypothesis using ten open-nesting bird species in Arizona, USA. Parental activity was greater during the nestling than incubation stage because parents visited the nest frequently to feed their young during the nestling stage. However, nest predation did not generally increase with parental activity between nesting stages across the ten study species. Previous investigators have found similar results. We tested whether nest site effects might yield higher predation during incubation because the most obvious sites are depredated most rapidly. We conducted experiments using nest sites from the previous year to remove parental activity. Our results showed that nest sites have highly repeatable effects on nest predation risk; poor nest sites incurred rapid predation and caused predation rates to be greater during the incubation than nestling stage. This pattern also was exhibited in a bird species with similar (i.e. controlled) parental activity between nesting stages. Once nest site effects are taken into account, nest predation shows a strong proximate increase with parental activity during the nestling stage within and across species. Parental activity and nest sites exert antagonistic influences on current estimates of nest predation between nesting stages and both must be considered in order to understand current patterns of nest predation, which is an important source of natural selection.

Keywords: parental provisioning rates; nest predation; Skutch's hypothesis; nest site effects

1. INTRODUCTION

Evolution of phenotypic traits is often constrained by costs that act in opposite proximate and evolutionary relationships. For example, Skutch (1949) hypothesized that nest predation increases proximately with the rate that avian parents visit the nest to feed their young (figure 1). This positive proximate function was expected to favour a negative evolutionary function; environmental conditions where nest predation risk is greater (e.g. lowland tropics or open nests) are thought to favour evolution of reduced parental activity (figure 1). Thus, parental activity and nest predation are hypothesized to show opposite proximate (positive) and evolutionary (negative) relationships, but these relationships have not been widely tested (Martin 1996a).

Past work on understanding parental provisioning rates has focused on the importance of chick demands from hunger within constraints of acceptable levels of parental effort (e.g. Briskie *et al.* 1994; Moreno *et al.* 1995; Kilner & Davies 1998; Wright *et al.* 1998; Kilner *et al.* 1999; Sanz & Tinbergen 1999). Skutch's (1949) hypothesis places an alternative emphasis on nest predation as a constraint on differences in parental provisioning rates (Martin 1996a; Martin *et al.* 2000). Recent studies have provided broad evidence for the negative evolutionary pattern (see figure 1), where species at higher risk of nest predation show lower parental activity (Martin & Ghalambor 1999; Conway & Martin 2000; Martin *et al.* 2000). Yet, such results should derive from a positive proximate response; nest predation should increase proximately with parental

activity in order to favour the evolutionary pattern (figure 1).

Recently, investigators have argued against such proximate costs; nest predation did not increase in the nestling stage when parents visited the nest more often compared with the incubation stage (Roper & Goldstein 1997; Lloyd 1998; Farnsworth & Simons 1999). These authors argued that Skutch's (1949) hypothesis could therefore be rejected. Yet this approach assumes that parental activity is the only factor influencing differences in predation rates between nesting stages. Variation in nest site quality can often influence nest predation (Martin & Roper 1988; Kelly 1993; Martin 1996b, 1998; but see Holway 1991; Howlett & Stutchbury 1997) and such effects could mask parental activity effects on nest predation; if nests in poor sites are found quickest (i.e. in incubation) by predators, such effects could increase predation rates during the incubation stage compared with the nestling period. Nest predation rates are less in the nestling stage than during incubation for many species (see the review in Martin 1992b). This decrease in nest predation between stages must have an environmental cause and nest site effects are a logical possibility.

Four alternatives are possible (figure 2). The null hypothesis is that neither parental activity nor nest sites influence predation risk between nesting stages, thereby yielding no difference in observed predation rates between stages (figure 2a). One alternative is that nest sites have no effect but parental activity causes increased predation in the nestling stage (figure 2b). Another possibility is that parental activity effects do not exist and that nest site effects cause nest predation to decrease in the nestling stage compared with incubation (figure 2c). Finally, both nest sites and parental activity may

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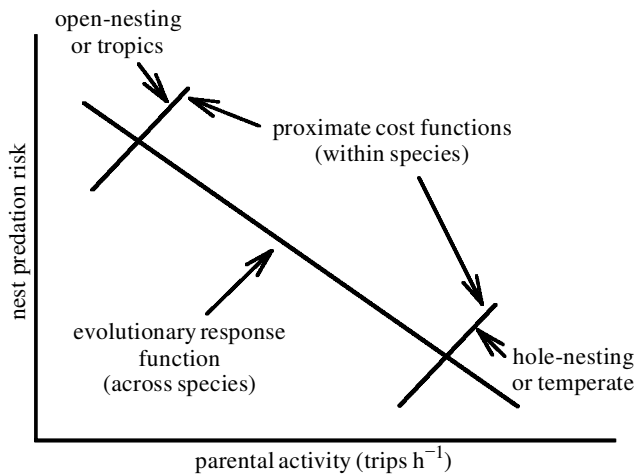


Figure 1. Skutch's (1949) hypothesis is based on opposite proximate and evolutionary relationships (Martin 1996a; Martin *et al.* 2000). Nest predation is expected to increase with parental activity within species yielding positive proximate cost functions within species or populations. Species or populations in environmental conditions with higher ambient levels of nest predation (e.g. open nests versus hole nests or lowland tropical versus temperate locations) should evolve lower activity (numbers of trips to the nest per hour), yielding a negative evolutionary function across species or populations.

influence predation, causing them to offset each other such that observed predation rates do not differ between stages (figure 2*d*).

We tested these alternatives using ten open-nesting passerine bird species that coexist in Arizona, USA. We restricted our test to open-nesting species because variation in their mean clutch size (3.7–4.4 eggs) (Martin 1995) is restricted, thereby minimizing this confounding effect on provisioning rates. First, we compared parental activity and nest predation rates between incubation and nestling stages to examine whether nest predation generally increased with activity between stages. Then we conducted an experiment that removed parental activity effects in order to test nest site effects. Finally, we examined whether predation increased proximately with parental activity once any nest site effects were controlled.

2. STUDY AREA AND METHODS

The study sites were 22 high-elevation forest drainages of mixed conifer and deciduous canopy species in Arizona. Dominant trees included *Pinus ponderosa*, *Populus tremuloides*, *Pseudotsuga menziesii*, *Pinus strobiformes*, *Abies concolor*, and *Quercus gambelii*. *Robinia neomexicana*, *Acer grandidentatum* and young canopy trees dominated the understory (see Martin (1998) for details). The primary nest predators (Martin 1996*b*) were red squirrel (*Tamiasciurus hudsonicus*), gray-necked chipmunk (*Eutamias cinereicollis*), house wren (*Troglodytes aedon*) and Steller's jay (*Cyanocitta stelleri*).

We examined parental activity and nest predation rates for all of the common open-nesting species on our study sites. These included the hermit thrush (*Catharus guttatus*), American robin (*Turdus migratorius*), yellow-rumped warbler (*Dendroica coronata*), MacGillivray's warbler (*Oporornis tolmiei*), red-faced warbler

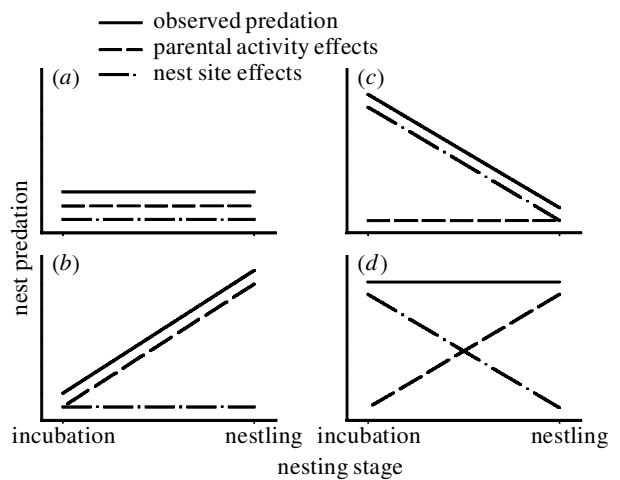


Figure 2. Possible alternative effects of nest sites and parental activity on observed nest predation rates between nesting stages of birds. (a) No effect of either factor on observed predation. (b) No effect of nest site, but an increase in observed predation during the nestling stage because of increased parental activity. (c) No effect of parental activity, but a decrease in observed predation during the nestling period because nest site effects cause the most obvious nests to be depredated earliest. (d) Antagonistic effects of parental activity and nest sites causing them to offset each other and yield no differences in observed predation between nesting stages.

(*Cardellina rubrifrons*), Virginia's warbler (*Vermivora virginiae*), orange-crowned warbler (*Vermivora celata*), green-tailed towhee (*Pipilo chlorurus*), gray-headed junco (*Junco hyemalis*) and western tanager (*Piranga ludoviciana*). Study drainages were searched for nests from the beginning of May until the end of July in 1988–1998. Nests were located by following adults as described by Martin & Geupel (1993).

Birds were videotaped during their incubation and nestling periods from 1993 to 1998 using video cameras with a $\times 20$ –40 zoom placed at least 5 m from nests for the first 6 h of the day beginning 30 min before sunrise (Martin & Ghalambor 1999; Martin *et al.* 2000). This protocol standardized both time of day and sampling duration in order to provide data on parental activity. All video recordings during the nestling period were made one or two days after primary feathers broke their sheaths in order to control for stage of development. The videotapes were scored for the number of trips to and from the nest by both parents (Martin & Ghalambor 1999; Martin *et al.* 2000). The number of trips per hour was averaged over the 6 h of monitoring for each nest and then averaged across nests in order to obtain mean values for each species. We obtained parental activity data from a minimum of 5 nests per species per nesting stage (minimum = 5 nests \times 6 h \times 2 stages), but generally obtained larger samples, averaging 25.1 nests per species during incubation and 23.7 nests per species during the nestling stage.

The date and status of each nest was recorded every three to four days. Nests were checked from a distance using binoculars whenever possible. If parents were on the nest it was recorded as active, but if parents were absent the nest was approached in order to verify its status and contents. Human visitation does not appear to influence predation probability in the system we used (Martin and Roper 1988; T. E. Martin, unpublished data). Nests that fledged at least one young were considered successful. Depredation was assumed when the eggs or nestlings (when too

young to fledge) disappeared (Martin 1998). Daily predation rates for predation events only were estimated following Mayfield (1975) and Hensler & Nichols (1981). Daily predation rates were calculated for the incubation and nestling stages separately by dividing the number of depredated nests by the total observation days for all nests for each period. The sample sizes ranged from 92 to 451 nests per species (mean = 268 nests).

In order to test for possible nest site effects on predation rates and establish a null pattern of differences between the incubation and nestling stages independent of parental activity (i.e. figure 2*a,c*), we used real nests of the four ground-nesting species (orange-crowned warbler, Virginia's warbler, red-faced warbler and gray-headed junco) from the previous year on all 22 plots. We used nest sites of ground-nesting birds because these species are abundant and because they place their nests in depressions under the stems of wood plants thereby allowing the nests to be located in subsequent years. Nests of off-ground-nesting birds, on the other hand, are destroyed over winter by snow and other harsh weather leaving insufficient nests for conducting rigorous experiments. Nests of ground-nesting species were marked with flagging after the young had fledged or the nest was depredated in order to allow mapping of nest sites at the end of each season. In addition, the location of each nest was described on nest cards relative to permanent station markers. Both flagging and nest descriptions allowed nests to be found in the season after they were constructed and used by the bird. We could not find all nests in subsequent years for differing reasons, such as lack of flagging or poor descriptions. In addition, only ca. 75% of nests were found in each season. Finally, we used only half of the nests at any one time (see below). As a result, we only added one to two (rarely three) experimental nests to any plot at any one time. Given that the plots were 25–50 ha in size, then these experimental nest sites were generally quite distant from each other (i.e. usually more than 100 m) and did not add substantially to the densities of real nests on these sites.

We placed two zebra finch (*Taeniopygia guttata*) eggs in these year-old nests and left them exposed to predators for 15 days, but checked whether they had been eaten by a predator every three to four days (i.e. the same protocol used for real nests occupied by birds; see above). This approach allowed examination of nest predation at real nest sites, but with parental activity effects removed. We divided nests into three groups based on their original fate when occupied by the bird: (i) nests that were depredated during incubation, (ii) nests that were depredated during the nestling stage, and (iii) nests that successfully fledged young. We calculated daily predation rates for each group separately. We conducted this experiment in 1998 using 92 ground nests from 1997. We repeated the experiment in 1999 using 86 new nests from 1998 and we repeated the tests on 77 nests from 1997 because of differences in temporal replicates in 1998 (see below). Half of the nest sites were tested at any one time in each year such that eggs were placed out twice in each year, i.e. at the end of May and at the end of June. Thus, we had two temporal replicates for each of the three tests (1997 nests tested in 1998, 1997 nests tested in 1999 and 1998 nests tested in 1999) for a total of six replicates using 255 nests. The six replicates differed in their nest predation rates for the group of nests that were depredated during the nestling period ($\chi^2 = 10.8$, $p = 0.055$ and d.f. = 5) and those that were successful ($\chi^2 = 16.5$, $p = 0.0055$ and d.f. = 5), but not for the group of nests that were depredated during incubation ($\chi^2 = 4.6$, $p = 0.47$ and d.f. = 5). The differences resulted from higher predation rates in the second replicate of 1997 nests tested in 1998. When this replicate

was removed, the remaining five replicates did not differ from each other in nest predation rates within any of the three fate groups, i.e. incubation predation ($\chi^2 = 1.7$, $p = 0.79$ and d.f. = 4), nestling predation ($\chi^2 = 2.4$, $p = 0.66$ and d.f. = 4) and successful ($\chi^2 = 3.2$, $p = 0.52$ and d.f. = 4), so we therefore pooled them as follows. In order to eliminate any pseudo-replication from testing 1997 nests in both 1998 and 1999, we pooled the tests of the 1997 and 1998 nests tested in 1999. Our second test pooled 1997 nests tested in 1998 with 1998 nests tested in 1999. We conducted these tests with the second replicate in 1998 both present and removed because the second replicate of 1997 nests tested in 1998 differed from other replicates (see above).

Differences in parental activity and daily predation rates between incubation and nestling stages were tested using a paired *t*-test across all species in order to examine general relationships. Differences for experimental nests in daily predation rates among replicates within and between years were first tested for each of the three nest fate categories (depredated in incubation, depredated in nestling and successful). We pooled those replicates (three of the four) that did not differ from each other within a stage to then test for differences between stages. These tests of daily predation rates were based on the program CONTRAST (Hines & Sauer 1989). This program uses a χ^2 -approach that is analogous to ANOVA in order to control for experiment-wise error and adjust for type I errors (Hines & Sauer 1989).

We used Pearson correlations for testing correlations between parental activity and nest predation. We tested for a positive correlation across species between the change in parental activity and nest predation based on the relative change in these two parameters between nesting stages (nestling–incubation). Although this test was conducted across species, it was a proximate test because we were testing the hypothesis that species with greater increases in activity in the nestling stage should show greater increases in nest predation between stages. We tested for any phylogenetic effects using independent contrasts (e.g. Felsenstein 1985; Harvey & Pagel 1991). We used a phylogenetic hypothesis described previously (Martin 1995) and forced these regressions through the origin (Harvey & Pagel 1991).

3. RESULTS

Parents visited nests at higher rates (paired *t*-test, $t = 6.6$, $p < 0.0001$ and d.f. = 9) during the nestling period (7.4 ± 0.8 trips h^{-1}) than during incubation (3.3 ± 0.2 trips h^{-1}), but species varied in the extent of relative changes. Some species, such as the hermit thrush showed relatively little change in activity between stages, while other species, such as the western tanager showed large changes (figure 3*a*). On the other hand, daily predation rates differed only marginally (paired *t*-test, $t = 2.28$ and $p = 0.048$) between the incubation (0.036 ± 0.005) and nestling (0.027 ± 0.003) stages across all species (figure 3*b*). This marginal result exists because species showed differing patterns. The biggest difference between stages was that some species, such as the hermit thrush and green-tailed towhee, showed much greater nest predation in the incubation stage than in the nestling period (figure 3*b*). Other species showed little difference between stages (e.g. orange-crowned warbler), while a few species showed slightly higher predation in the nestling stage than in incubation (e.g. western tanager). In general, however, changes in nest predation in the

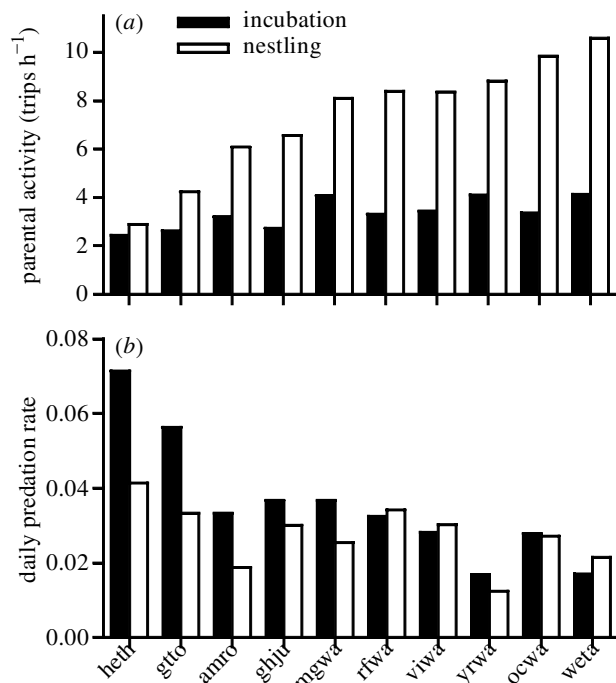


Figure 3. (a) Parental activity (number of trips to the nest per hour) during the incubation and nestling (one to two days after pin feathers broke their sheaths to control for stage of development) stages for open-nesting bird species on high elevation sites in Arizona, USA. (b) Daily predation rates (the probability that a nest is depredated per day) for the incubation and nestling stages. Species are arranged in order of increasing activity during the nestling period. Species: heth, hermit thrush; gtto, green-tailed towhee; amro, American robin; ghju, gray-headed junco; mgwa, MacGillivray's warbler; rfwa, red-faced warbler; viwa, Virginia's warbler; yrwa, yellow-rumped warbler; ocwa, orange-crowned warbler; weta, western tanager.

nestling period compared with incubation did not follow expectations based on changes in parental activity (i.e. figure 2*b*); the higher activity of parents in the nestling stage (figure 3*a*) was not met by generally higher nest predation (figure 3*b*).

We tested experimentally as to whether nest predation differed between nesting stages when parental activity was controlled (i.e. figure 2*a,c*). We placed eggs in nests constructed by birds in the previous year in order to examine nest predation relative to their prior nest fate. When we pooled (see §2) nests from 1997 and 1998 that were tested in 1999 (figure 4*a*), nest predation rates differed strongly among the three nest fate groups ($\chi^2 = 16.9$, $p = 0.0002$ and d.f. = 2). Similarly, when we pooled nests from 1997 that were tested in 1998 with 1998 nests that were tested in 1999 (figure 4*b*), nest predation rates also differed strongly among the three nest fate groups ($\chi^2 = 13.9$, $p = 0.001$ and d.f. = 2) and when the second replicate in 1998 was removed ($\chi^2 = 15.5$, $p = 0.0004$ and d.f. = 2). The pattern in every case was higher predation in nests that were depredated during incubation than nests that were more successful in the prior year (figure 4). These experimental results indicate a null pattern (independent of parental activity) of greater predation during incubation than the nestling

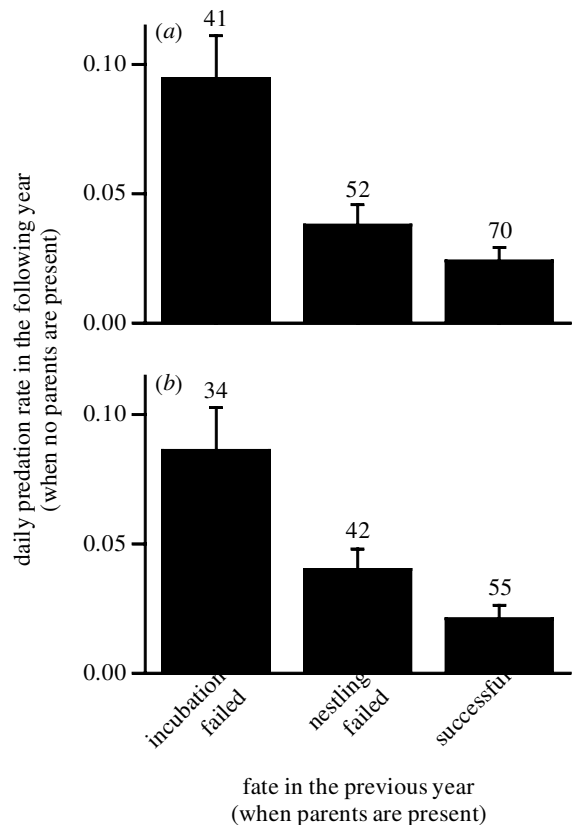


Figure 4. Daily predation rates (\pm s.e.) for nests of ground-nesting birds (gray-headed junco, red-faced warbler, orange-crowned warbler and Virginia's warbler) that were baited with zebra finch eggs in the year following their construction and use by birds but when parents were no longer present to influence predation rates. The nests were classified into three groups based on their fate when used by birds: (i) nests that were depredated during incubation, (ii) nests that were depredated during the nestling stage, or (iii) nests that were successful. (a) Nests constructed in 1997 and 1998 and tested in 1999. (b) Nests constructed in 1997 and tested in 1998 plus nests constructed in 1998 and tested in 1999. The second temporal replicate in 1998 was removed because it differed from the remaining replicates (see §2). Numbers above bars indicate the numbers of nests sampled.

period due to nest site effects. This result was verified further by comparing nest predation in the incubation and nestling stages for the hermit thrush, a species where parental activity was similar (i.e. controlled) between stages (figure 3*a*). The hermit thrush showed the same strong decrease in nest predation ($\chi^2 = 11.9$ and $p = 0.0006$) from incubation to nestling stage (figure 3*b*) as observed with the experimental nests (figure 4).

These results for both the experimental nests of ground-nesting species as well as the real data for an off-ground-nesting species (i.e. the hermit thrush) provided a baseline null pattern expectation that, when parental activity is controlled, predation should be less during the nestling period than in incubation. If nest predation increases proximately with increases in parental activity, then species with small changes in parental activity between stages (i.e. species to the left in figure 3*a*) should show nest predation differences that are similar to those

found in the experiment (i.e. a strong decrease) (figure 4), whereas species with greater increases in parental activity (i.e. those further to the right in figure 3*a*) should have greater increases in nest predation relative to incubation, thereby potentially offsetting the nest site effects. We tested this prediction by examining changes in predation and activity levels between stages by subtracting incubation period data from nestling period data. We found that species with larger increases in parental activity during the nestling stage showed increasingly greater increases in nest predation (figure 5) and this correlation remained when phylogeny was controlled ($r = 0.86$, $p = 0.001$ and $n = 9$ independent contrasts). Some species increased their parental activity during the nestling period to a sufficient degree as to offset nest site effects completely and yielded no difference or even slight increases in nest predation during the nestling stage compared with during incubation (figures 4 and 5).

4. DISCUSSION

Skutch's (1949) hypothesis is important because it brings an alternative perspective to the evolution of parental care behaviours, which is a widely studied subject (e.g. Clutton-Brock 1991). Feeding rates by parents have been considered primarily in terms of hunger of the young and energy constraints on the parents (e.g. Briskie *et al.* 1994; Moreno *et al.* 1995; Kilner & Davies 1998; Wright *et al.* 1998; Kilner *et al.* 1999; Sanz & Tinbergen 1999). The notion that nest predation may place a critical evolutionary constraint on variation in feeding rates among species has been overlooked, but these constraints appear to be strong (Martin *et al.* 2000). Yet such evolutionary effects should derive from proximate costs where nest predation increases with parental activity within species (Martin 1996*a*).

Parental activity is typically greater when feeding young than during the incubation period (figure 3*a*), yielding an expectation under Skutch's (1949) hypothesis of increased predation during the nestling period if nest site effects are non-existent (i.e. figure 2*b*). We found that nest predation was not greater during the nestling stage (figure 3*b*), as has also been found previously by others (e.g. Roper & Goldstein 1997; Lloyd 1998; Farnsworth & Simons 1999; see also the review in Martin 1992*b*). On the surface, these results could argue against a proximate cost function between nest predation and parental activity (Roper & Goldstein 1997; Lloyd 1998; Farnsworth & Simons 1999), but such conclusions assume that nest sites do not influence differences in predation risk between stages.

Our results show that nest sites have very clear effects on nest predation rates (see also Martin & Roper 1988; Martin 1998); nests that had a high risk of predation in one year had a remarkably consistent high risk in the subsequent year (figure 4), presumably because they are poor sites. Of course, variation existed such that some of the nests that failed in the previous year were successful in the experiment. Nonetheless, repeatability was strong, causing highly vulnerable nests to be lost quickly (see figure 4) and yielding greater predation during incubation than the nestling stage when parental activity was controlled (i.e. figure 2*c*). Moreover, data for the hermit

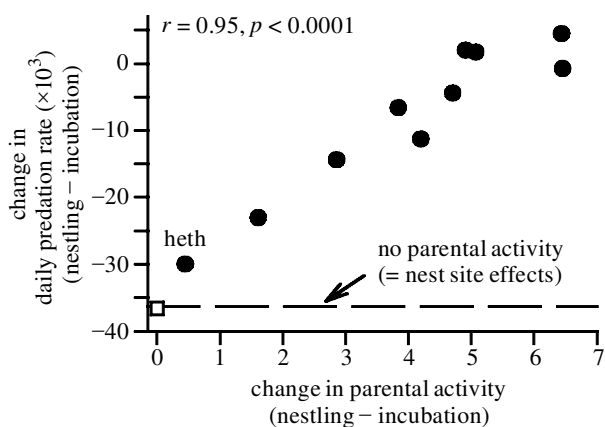


Figure 5. Correlation for ten open-nesting bird species (as identified in figure 3) between the change (difference between nestling period minus incubation period) in parental activity versus daily predation rates. Experiments that removed the effects of parental behaviour (see figure 4) established the baseline point (open square) and axis (dotted line) for ground-nesting species, but were not included in the correlation. The hermit thrush (heth) is identified as an off-ground-nesting species with the least difference in parental activity between stages.

thrush supported this conclusion, showing the same declining predation pattern (see figure 3*b*) in a species where parental activity was effectively controlled (i.e. similar) between nesting stages (see figure 3*a*). Thus, simple comparisons of nest predation between nesting stages are inappropriate tests of Skutch's (1949) hypothesis because nest site effects can strongly influence the expected pattern of predation.

The dotted line in figure 5 represents the axis of origin for examining the effects of parental activity when nest site effects for ground-nesting species were removed. This baseline or a very similar one seems to apply to off-ground-nesting species as well. The off-ground-nesting hermit thrush increased parental activity only slightly in the nestling period compared with during incubation (figure 3*a*) and the difference in nest predation was only slightly above the experimental results (figure 5). When considered from this baseline, all species showed increased nest predation with parental activity between stages (figure 5). Although this test was across species, it is a proximate test because it tests the proximate change in predation related to change in activity within species. However it extended the test to examine whether species that exhibited greater increases in activity (i.e. the right side of figure 3*a*) incurred greater proximate increases in nest predation. The proximate response was very clear and yielded a strong positive relationship (figure 5), as hypothesized by Skutch (1949). Similarly, pairs with higher activity in the incubation stage alone had a higher probability of nest predation for three Parulid species (Martin *et al.* 2000). Because parental activity acts antagonistically to nest site effects for changes in nest predation between nesting stages (i.e. figure 2*d*), the observation of no difference in nest predation between nesting stages does not refute Skutch's (1949) hypothesis. Instead, as we show here, it can actually reflect a strong proximate effect of parental activity offsetting antagonistic nest site effects.

Ultimately, nest predation can exert strong selection on a wide variety of phenotypic traits (Skutch 1949; Slagsvold 1982, 1984; Martin 1992*a*, 1995, 1998; Redondo & Castro 1992; Bosque & Bosque 1995; Briskie *et al.* 1999; Conway & Martin 2000; Ghalambor & Martin 2000; Martin *et al.* 2000) making identification of the ecological factors that influence the risk of nest predation necessary. Previous work has suggested that nest site selection within species as well as differences in nest types between species are important determinants of variation in nest predation risk (e.g. Martin 1993, 1995, 1996*b*, 1998). Conversely, however, the proximate effects of parental activity attracting predators could influence the evolution of nest site choices, favouring the choice of more protected sites in species that are more exposed in their foraging and which have an increased probability of attracting predators (Alerstam & Högstedt 1981, 1985; Greenwood 1985). Such potential interactions begin to weave a picture of complex interactions. For example, our results here show that observed nest predation rates are not a simple function of nest sites, but a more complex interaction of parental activity and nest site effects (also see Kelly 1993). Moreover, parental activity effects may exert complex influences on current rates of nest predation because of the opposing action of proximate and evolutionary relationships. We show here that increased parental activity can increase predation risk in a proximate context. Yet, species that are at greater risk of nest predation because of factors such as nest type evolve reduced parental activity (Skutch 1949; Martin 1996*a*; Conway & Martin 1999; Martin & Ghalambor 1999; Martin *et al.* 2000), which should yield a proximate reduction in nest predation rates. These opposing proximate and evolutionary relationships between parental activity and nest predation may offset each other during the nestling period and blur patterns of nest predation among nest sites or other ecological conditions. Thus, measurement of nest predation as a selective force needs careful consideration. Such proximate and evolutionary considerations have been neglected, but clearly deserve more attention in understanding variation in measured nest predation and its influence on the evolution of parental care behaviours and other phenotypic traits.

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