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## VICINITY OF SPARROWHAWK NEST AFFECTS WILLOW TIT NEST DEFENSE<sup>1</sup>

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*Key words:* Willow Tit; *Parus montanus*; Sparrowhawk; Accipiter nisus; predation; nest defense; parental investment; experience.

Offspring defense from predators is an important component of parental investment (Trivers 1972). Predation is a strong selective pressure and organisms with parental care often enhance the survival chances of their offspring by defending these from potential predators (e.g., Gottfried 1979, Brunton 1990). Offspring defense of breeding animals includes alarm calling, distraction displays, threat or attack responses (e.g., Bjerke et al. 1985, Montgomerie and Weatherhead 1988). Beside the increased benefits (Anderson et al. 1980, Greig-Smith 1980, Blancher and Robertson 1982, Brunton 1990), defense behavior also has its costs due to injuries or death (Curio and Regelman 1985, 1986; Montgomerie and Weatherhead 1988; Brunton 1990). The costs of defense are therefore strongly affected by the danger of the predator towards which the responses are directed. When optimizing nest defense behavior, the defender should take into account the capabilities of

the predator (e.g., Brunton 1990) and then adjust the level of defense according to the expected benefits and costs (Montgomerie and Weatherhead 1988). Animals may have innate information of the potential danger of different predators, and they can learn this from experience (Curio 1978, Curio and Regelman 1985).

Experience with predators can theoretically have various effects on parental nest defense behavior. Parental investment theory predicts at least four different patterns. (I) If parents learned about the capabilities of the predator during frequent encounters, experienced parents would be able to undergo higher defense intensity than inexperienced birds with the same risk-level (Montgomerie and Weatherhead 1988). (II) If frequent encounters did not lead to a real threat for the parent or the offspring of being preyed upon, parents might learn that the risk, and consequently, the costs of defense are decreased. This would then favor increased nest defense intensity with experience (Coleman 1987, Montgomerie and Weatherhead 1988). Alternatively, Knight and Temple (1986) argued that "positive reinforcement" and "loss of fear" could explain increased defense intensity with experience without any cost/benefit analyses (but see Coleman 1987, Rytkönen et al. 1990). Alternatively, frequent encounters with a predator may also increase risk for the parent or the offspring, since predators can increase their

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TABLE 1. The mean ( $\pm$ SD) average and minimum approach distances, calling rates and the numbers of movements around the predator model of Willow Tit parents in two nest defense experiments. The number of nests tested were 24 in experiment 1 and 14 in experiment 2.

Predator model	Average distance (m)	Minimum distance (m)	Calling rate calls/min	Number of movements
Experiment 1				
Sparrowhawk	5.8 $\pm$ 3.1	3.3 $\pm$ 2.2	19.8 $\pm$ 6.5	3.4 $\pm$ 2.1
Stoat	2.6 $\pm$ 2.6	1.0 $\pm$ 1.5	16.9 $\pm$ 5.4	7.1 $\pm$ 5.4
Experiment 2				
Pygmy Owl	2.6 $\pm$ 1.3	1.0 $\pm$ 0.6	19.8 $\pm$ 5.2	5.5 $\pm$ 3.0
Stoat	2.1 $\pm$ 1.7	0.9 $\pm$ 1.0	16.8 $\pm$ 5.8	8.0 $\pm$ 6.3

predation efficiency in patches, such as a territory or a nest-site where the prey is easily found (area concentrated search, see e.g., Sonerud 1985). (III) Thus, if the predation risk of parents increased, parents should show lower nest defense intensity with increased number of predator encounters (e.g., Knight 1984). (IV) Respectively, if the predation risk of offspring increased, parents should engage in higher defense intensity with experience (Bjerke et al. 1985). When examining these hypotheses, possible habituation effects must also be considered, although habituation can hardly be an anti-predatory adaptation (e.g., Coleman 1987).

In this study, we tested how the vicinity of the nest of a potential predator affected the nest defense behavior of Willow Tits (*Parus montanus*). The basic assumption (based on field observations) in this study was that the number of encounters with the predator is greater the shorter the distance between the nests of Willow Tits and the nearest predator. Thus, by knowing these distances, we could test the above hypotheses of the effect of predator experience on Willow Tit defense behavior. The potential predators studied were the Sparrowhawk (*Accipiter nisus*) and the Pygmy Owl (*Glaucidium passerinum*), both of which are predators of Willow Tit parents during the breeding season but only the Pygmy Owl of the Willow Tit nestlings.

## METHODS

This study was conducted near Oulu, northern Finland (65°N, 25°30'E) in 1992. The field area consists of mainly coniferous and mixed deciduous forests. For detailed description of the study area see Orell and Ojanen (1983). Willow Tits breed in holes they excavate each year in decaying stumps, mostly of birch (*Betula* sp.). Willow Tits also accept stumps that are removed and attached on other trees in areas where there is a short of natural stumps. All the nests of Willow Tits, Sparrowhawks and Pygmy Owls were located on the area of 22 km<sup>2</sup>. After the nests of the predators were located, we chose the tit nests to be tested in a way that the predator nests outside the study area could not have any effect on the studied Willow Tits' behavior.

At each Willow Tit nest, the parental defense behavior was tested towards either a model of Sparrowhawk or Pygmy Owl, and towards a stoat (*Mustela erminea*) for control. These two trials were done at the end of the nestling period on different days. At a trial the predator model was placed about 0.5 m in front of

the nest entrance. The distances of the male and female parents from the model were continuously determined during a 5-min period, and the number of movements of each parent around the predator model were registered. The alarm calls of the birds were also recorded (into C-cassettes). The method has been described in detail in Rytkönen et al. (1990, 1993).

The tapes were analyzed later (computer aided), and the nest defense behavior was described by four variables: (1) the average and (2) the minimum approach distance of the parent from the predator model, (3) the alarm calling rate (calls/min), and (4) the number of movements around the predator model (movements/min) during the trial. We assume that the parent bird took the greater risk the nearer it approached the predator model, and the more it gave alarm calls and moved around the predator. Since all the offspring in a nest benefited equally from a unit of parental care ("unshared" parental investment of Lazarus and Inglis 1986), we could directly compare the nest defense behavior of the parents.

The Sparrowhawk is not a predator of tit nestlings. Therefore, we compared the responses of tits at the nest ( $n = 39$ ) and in the winter 1993 ( $n = 10$ ). The average approach distances ( $t = 4.11$ ,  $P < 0.001$ ) and the calling rates ( $t = 3.49$ ,  $P < 0.01$ ) showed significantly more vigorous responses in the breeding season. Minimum distances and movements showed no significant pattern. Thus, responses towards the Sparrowhawk at the nest can be considered nest defense behavior, which may inform the predator that it is detected and that its hunting chances are diminished. The benefits of this behavior can be measured, for example, with the reduced time for the parents of being off-duty in nestling provisioning (e.g., Curio 1978).

The appropriate method for studying the relationship between nest defence intensity and distance to nearest predator nest would be Model II regression (e.g., Sokal and Rohlf 1981). However, the methods for this have not yet been agreed upon. On the other hand, we think we could test the above hypotheses also by applying Model I regression, though realizing that we might have underestimated type I error.

## RESULTS

There were four nests of Sparrowhawks in our field area. The tested Willow Tit nests ( $n = 24$ ) located 0.08–1.1 km (median 0.56 km) from the nearest hawk nest.

TABLE 2. The relationships between Willow Tit nest defense intensity (average and minimum approach distances, alarm calling rate and number of movements around the predator model) and distance to the nearest Sparrowhawk nest, as revealed by Model I regressions (see Methods). (A) experiments with Sparrowhawk as a predator model (for females  $n = 21$ , for males  $n = 18$ ). (B) experiments with Stoat as a predator model ( $n = 21$  for both sexes). All variables except calling rates were ln-transformed ( $P$ -values are indicated only for the slopes).

Sex	Parameters	Average distance	Minimum distance	Calling rate	Number of movements
(A) Sparrowhawk					
Females	Intercept	3.39	2.86	-9.49	-1.27
	Slope	-0.26*	-0.24*	4.80*	0.42*
	$R^2$	0.20	0.19	0.19	0.27
Males	Intercept	3.30	2.33	26.57	1.30
	Slope	-0.23	-0.16	-1.12	0.02
	$R^2$	0.08	0.03	0.02	0.00
(B) Stoat					
Females	Intercept	0.44	0.01	1.73	2.77
	Slope	0.12	0.10	2.35	-0.16
	$R^2$	0.02	0.01	0.11	0.02
Males	Intercept	0.35	-0.36	11.64	3.25
	Slope	0.11	0.13	0.99	-0.24
	$R^2$	0.02	0.04	0.02	0.06

\*  $P < 0.05$ .

Six observations of naturally occurring tit-hawk encounters were done at nests located 0.2–0.5 km from the nearest Sparrowhawk nest. The average nest defense responses of male and female Willow Tits towards the Sparrowhawk and stoat models are presented in Table 1.

The nest defense intensity of Willow Tit females towards a Sparrowhawk model were affected by the vicinity of Sparrowhawk nest: the average and minimum approach distances were the longer, the alarm calling rates the lower, and the number of movements fewer the closer to the predator nest tits bred (Table 2a). These responses suggest that the nest defence intensity was decreased when the number of encounters with Sparrowhawks increased (hypothesis III). The vicinity of Sparrowhawk nest did not affect the female responses towards the stoat (Table 2b), suggesting that experience with predators was predator-specific. On the other hand, all male responses were independent of the distance to the Sparrowhawk nest (Table 2a, b).

There was only one nest of Pygmy Owl in our field area. The tested Willow Tit nests ( $n = 14$ ) located 0.16–1.36 km (median = 0.91 km) from the owl nest. No tit-owl encounters were observed. The nest defence responses towards Pygmy Owl were generally more intense than those towards Sparrowhawk (Table 1). The nest defence intensity of male and female Willow Tits towards the Pygmy Owl or the stoat were not affected by the vicinity of Pygmy Owl nest (Model I Regression: for slopes all  $P > 0.10$ ).

## DISCUSSION

Female Willow Tits significantly decreased their nest defense intensity the closer their nests were to the nearest Sparrowhawk nest. It is spatially obvious and our field observations also indicate that tits breeding close

to a Sparrowhawk nest encounter the hawk more frequently than tits breeding further away. The specificity of the above responses to the Sparrowhawk nest distance was confirmed by the control experiment: no corresponding dependency on hawk-nest-distance was found in responses towards Stoats. Therefore, the above result conforms to the prediction of the hypothesis that frequent encounters with a predator increases the predation risk of the tit parents at the nest-site. Newton (1986) found that tits breeding in the vicinity of the Sparrowhawk nest are more vulnerable to predation than tits breeding further away. Thus, as the costs of defense increase, decreased defense level should be favored in the vicinity of Sparrowhawk nest (e.g., Montgomerie and Weatherhead 1988). Corresponding results have been found by Knight (1984) in ravens (*Corvus corax*): birds breeding in areas of high human densities (farmland) were more timid nest defenders and showed stronger avoidance behavior towards humans than ravens breeding in areas of low human densities (rangeland). This, he argued, was because humans destroyed a considerable proportion of the nests and shot parent birds in farmlands, whereas the ravens could breed safely in rangeland.

The behavior of female Willow Tits against Sparrowhawks did not support the hypotheses predicting increased defense intensity with predator experience (hypotheses I, II, and IV). Alternatively, the responses of males towards Sparrowhawk, and the parental responses towards Pygmy Owl were not dependent on the distance to the nearest predator nest. These responses are difficult to interpret with the above hypotheses. The Pygmy Owl results might, however, be explained by the difference in activity times between tits and owls. Although the Pygmy Owls are also day-active during the breeding season, their most active hunting periods are between sunset and sunrise (Mik-

kola 1983). During the breeding season, Willow Tits start their activity a few hours after sunrise and finish it a few hours before sunset (Rytkönen et al., unpubl.), and thus the high activity times of tits and owls do not overlap. Daily activity of Sparrowhawks (Newton 1986) is similar to that of Willow Tits, and therefore, the encounters between tits and hawks are much more obvious than between tits and owls.

However, if the encounters between tits and Pygmy Owls were numerous near the owl nest, the predicted responses of Willow Tit parents would be complicated. The Pygmy Owl is a potential predator of both the Willow Tit parents and their nestlings (Mikkola 1983). Therefore, the predation risk with increased number of encounters would increase for both the parents and the young (according to the hypotheses III and IV, respectively). The respective predictions for the nest defense intensity would then be a decrease and an increase with increased predator experience. Thus, these predicted responses could contradict each other, and as a result, defense intensity could appear independent of the distance to the nearest owl nest. However, it is more probable that the tit-owl encounters were quite few, and therefore, the basic assumption was not true for this experiment. The number of tit nests in the vicinity of the owl nest were also quite few.

The female responses suggest that tit-hawk encounters were numerous at the tit nests close to the Sparrowhawk nest. This should apply for the Willow Tit males as well as for the females. Males, however, did not show the female-like responses in the vicinity of Sparrowhawk nest. An explanation for this might be that male behavior at the nest is not only offspring defense but also protection of his mate against predation (Rytkönen et al. 1995; Hogstad 1992, 1995; see also Curio et al. 1984). Male Willow Tits are generally more vigorous defenders than females (Rytkönen et al. 1993), and some direct observations have suggested that males can actively chase the female away from the vicinity of the predator model (Rytkönen et al. 1995). Males would benefit from the survival of their mates, since breeding success of old females (>1 year) is significantly higher than that of juvenile females, which are the most probable new mates in case the old female dies (Orell et al. 1994). Thus, male behavior may not be adjusted only to the predation risk, and therefore, the female-like dependency on the number of predator encounters would be weaker in males. Alternatively, or in addition, males, which are significantly larger in size and in better physical condition than females in the end of nestling period (Rytkönen et al. 1993), may not experience as great an increase in predation risk as females with increasing number of predator encounters. This would give some indirect support for the hypothesis that experienced males are better able to cope with the predator though the predation risk increases.

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### RENESTING BY SPOTTED OWLS<sup>1</sup>

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**Key words:** *Renesting behavior; Spotted Owl; Strix occidentalis; Great Horned Owl; Bubo virginianus; Barred Owl; Strix varia.*

Spotted Owls (*Strix occidentalis*) typically begin courtship in late February or early March and lay eggs in late March or April. Nest success is high in most years (typically 70–90%). Nest failures occur for a variety of reasons, including abandonment or breakage of eggs, predation on eggs or young, collapse of nest structures, and mortality of adults (Forsman et al. 1984; Forsman, unpubl. data). Documented cases of renesting after nest failure are rare. We found only two confirmed cases, one in New Mexico (Kroel and Zwank 1992) and one in Oregon (Lewis and Wales 1993). Here we describe three cases of renesting by Spotted Owls in Washington, and present information on the frequency of renesting by Spotted Owls on four study areas in Oregon and Washington.

The three cases of renesting by wild Spotted Owls included one in 1992 on the east slope of the Cascades Range, and two in 1994 on the Olympic Peninsula. In all three cases, the nesting birds were banded and were being monitored as part of a long-term demographic study. Two of the pairs were comprised of adult birds (3+ years old) and one pair included an adult female and 2-yr-old male.

In all three cases, pairs were initially confirmed as nesting in early April (range = 3–7 April). Nest failure occurred sometime between 3–29 April. In two cases, nest failure was confirmed based on the presence of

broken eggshells found in the nest or on the ground under the nest. In the third case, two eggs were seen in the nest, and then disappeared without a trace. Cause of nest failure was undetermined in all three cases.

In all three cases, females moved to a new nest after the first nest failed. Distances between the original nests and new nests were 0.35, 0.40 and 1.0 km. Renesting was initiated between 25 April and 12 May. These dates were based on sightings of females going into new nests or by estimating egg-laying dates based on plumage development of juveniles observed at the new nests (Forsman 1981). Although we were not sure of exact dates when second clutches were initiated, it appeared that the minimum and maximum period between failure and initiation of a new clutch was about 14 and 30 days, respectively. Renesting produced two young at one site (estimated fledging date 15 July) and one young at another site (fledging date 6 July). At the third site, a single fledgling was found dead below the new nest on 13 July.

The three cases of renesting described above were the only instances of renesting observed in 221 cases of apparent nest failure on our study areas in Washington and Oregon between 1985–1994 (Table 1). This suggests that renesting occurred about 1.4% of the time after an initial failure. This estimate of renesting rate should be considered only an approximation, because some cases of apparent nest failure could have been cases where pairs acted like they were nesting but never actually laid eggs. It is also possible that some cases that were labeled as nest failures were actually cases where juveniles fledged, but were killed before being confirmed.

Our observations, and those of Lewis and Wales (1993) and Kroel and Zwank (1992) suggest that re-

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