

Nest defence in an altricial bird with uniparental care: the influence of offspring age, brood size, stage of the breeding season and predator type

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This study examines factors affecting nest defence in Aquatic Warblers *Acrocephalus paludicola*, a passerine species with uniparental (female) care. Stuffed predators, the Hen Harrier *Circus cyaneus* and the Polecat *Mustela putorius*, were presented at nests at various stages of the breeding cycle throughout the breeding season. The intensity of nest defence increased as the breeding cycle progressed and the offspring value hypothesis explained this pattern better than the vulnerability hypothesis. The number of nestlings and time of the breeding season (date) did not affect the level of nest defence. The results suggest that the nest defence behaviour of Aquatic Warblers was predator-specific. As expected, females' defence behaviour towards the mammalian predator was more risk-prone than that towards the avian one: the Polecat was approached more closely with a greater number of flights. Also the vocalisations given towards the two predators were different: in the presence of the polecat, compared with the harrier, loud, conspicuous "trr" calls were more frequent.

1. Introduction

Since the appearance of Trivers' (1972) model of parental investment, which emphasised fitness costs and benefits of parental decisions, several hypotheses predicting variation in nest defence have been presented (review in Montgomerie & Weatherhead 1988, Redondo 1989, McLean & Rhodes 1992, Vinuela et al. 1995). So far, the best documented pattern found in studies of nest defence has been the increase in the intensity of parents' reaction to predators during the course of a nesting attempt (review in Montgomerie & Weatherhead 1988, McLean & Rhodes 1992). On the ultimate level this has been explained by the offspring value hypothesis and the vulnerability hypothesis. The offspring value hypothesis interprets

the escalation in nest defence as an adaptive response to increasing offspring value. The hypothesis predicts a gradual, exponential increase in the level of nest defence during the breeding cycle and a maximum response at nest-leaving (Montgomerie & Weatherhead 1988). According to the second hypothesis (Harvey & Greenwood 1978, Brunton 1990) the intensity of nest defence correlates with the vulnerability of offspring to predation which is an increasing function of their stage of development. For altricial species this model (Brunton 1990) predicts a flat defence response during incubation, a rapid increase just after hatching followed by a much slower increase with a peak just prior to fledgling.

Among other factors that might influence the level of defence, the most important ones seem to

be offspring number and the progress of the breeding season. Parent birds could be expected to defend large broods more vigorously than small ones, since the former bring higher fitness benefits (Regelmann & Curio 1983, Rytkönen et al. 1995). Montgomerie and Weatherhead (1988) suggested that the effect of clutch/brood size need not necessarily be found in species with uniparental care because relative risk and cost of defence for a single parent is greater. Most authors have argued that defence level should increase with the progress of breeding season due to declining re-nesting potential (Weatherhead 1989, Rytkönen et al. 1995). Yet, field studies have given weak support for this hypothesis: most have found either a seasonal decline in nest defence or a stable investment (review in Halupka & Halupka 1997).

Finally, several authors (e.g., Gochfeld 1984, McLean & Rhodes 1992) have suggested that the behaviour of nest-defending birds (kinds of displays) depends on the type of predator and its intensity is related to the threat that the predator poses to the displaying parent. Intruders that are more dangerous for adult birds are expected to evoke a weaker response, as the risk, and thus cost, of defence is higher.

In this study I examined the influence of characteristics of the offspring (their age and number), season and predator type (avian vs. mammalian) on nest defence in the Aquatic Warbler *Acrocephalus paludicola*. I tested which of the two hypotheses explaining the ultimate function of the "offspring age effect" better fit to the empirical data. The Aquatic Warbler has uniparental (female) care (Dyrzcz & Zdunek 1993a). This allowed me to test the prediction that in such species, the most risky elements of antipredatory displays will not vary in intensity with the offspring number (Lazarus & Inglis 1986, Montgomerie & Weatherhead 1988).

2. Material and Methods

The study was carried out in May–July 1990 in the marshes of the Biebrza River Valley (NE Poland). The study site was a sedge (*Carex* spp.) meadow with some sparse concentrations of bushes. It adjoined a dam that may have made the

area more accessible to terrestrial predators.

Cup-shaped and very well hidden nests of Aquatic Warblers are placed in sedge tussocks. Nest losses caused by predators are low (22.2% according to the Mayfield method; Dyrzcz & Zdunek 1993b). Most females raise two broods each season. In 1990, modal clutch size was 5 and the number of nestlings ranged from 2 to 6. The breeding season started in mid May and lasted till the end of July. On average, the incubation and nestling periods were, respectively, 12 and 15 days long.

Females were presented with two models of predators (stuffed specimens): the female Hen Harrier *Circus cyaneus* and the Polecat *Mustela putorius*. A stuffed male Reed Bunting *Emberiza schoeniclus*, a common species in the study area, was used in control experiments. Both, harriers and polecats prey on passerines' nests and adult birds (e.g., Witkowski 1989, Lode 1995, K. Schulze-Hagen pers. comm.), although terrestrial predators are supposed to pose much smaller threat to parents. Harriers are presumably the most important predators of Aquatic Warbler nests in the study area (Dyrzcz & Zdunek 1993b, A. Dyrzcz pers. comm.). Mustelids occurred in the study area (L. Halupka, unpubl. data) and might cause some nest losses.

A hundred experiments (45 Harrier, 45 Polecat, 10 Bunting) were performed at 58 nests of different females (the population was colour-ringed). To avoid the possible problem of reinforcement of birds due to "revisitation" of the nest by the same predator (Knight & Temple 1986), a given model was exposed only once at each nest. Thirty nine nests were exposed to both predator models and 12 to one. Bunting was presented at 7 separate nests as the only model and at 3 nests tested previously with the polecat or the harrier. The order of models' presentation and the test age for each nest were random. Successive exposures at the same nest were separated by an interval of at least 24 h.

It could be argued that, in fact, the majority of females were tested twice (first for the reaction to one predator and next for the reaction to the other) and this could affect their response. To check whether such an effect occurred, I compared average calling rates (the most variable behavioural measure with the biggest sample size) of two

groups of females to the same predator. The test revealed that females which were naive to the experimental procedure responded to the polecat with a similar intensity as females which were already tested for reaction to the harrier (ANCOVA controlling for the effect of offspring age: $F_{1,42} = 0.779$, $p = 0.392$). Likewise, completely naive females called to the harrier with the same intensity as females which were already tested with the polecat ($F_{1,44} = 0.037$, $p = 0.850$). Hence, there was apparently no effect of habituation for birds visited twice with two different models.

Two people organised each trial. After hiding the observer in a blind, the second person positioned the model and went away. At the nestling stage, models were placed when a female was out of view and during incubation females were generally flushed from the nest. Dummies were placed 2 m from and facing the nest. The Polecat model was placed on the ground while the Harrier dummy was attached to a 1 m long stick (Harriers sitting on such short poles were observed in the area). Half a minute after model placement (this allowed the second individual to leave the nest vicinity) a stopwatch was started. During subsequent 10 minutes the kind and number of calls, number of flights and minimum distance (to the nearest 0.5 m) at which the bird approached the model were recorded. Since females appeared at the nest up to 5 min after the beginning of experiment (most immediately after model placement), for each individual data from first 5 min of reaction were analysed. The intensity of nest defence was described by three behavioural measures: call rates (number of calls per minute), flight rates (number per minute) and minimum distance (in m) between the nest defender and the predator. During control experiments ($n = 10$) with the Reed Bunting females did not exhibit nest defence behaviour and were engaged in their usual activities (foraging, feeding the offspring). Some females remained hidden during the presentation of the predator, so their distance from the model was difficult to assess. This resulted in smaller sample sizes of minimum distances.

The three variables (offspring age, offspring number, season advancing), hypothesised to shape the antipredator behaviour, covaried. Therefore, to analyse the effect of a single variable on nest defence intensity, the partial product-moment

correlation had to be used (Sokal & Rohlf 1995). Confidence intervals for partial correlation coefficients were calculated with the bootstrap percentile method using 5 000 iterations (Wasserman & Bockenholt 1989, Efron & Tibshirani 1993; for the interpretation of confidence intervals in the light of statistical power analysis see Steidl et al. 1997). The bootstrap method was also used to compare the rates of increase in intensity of nest defence around hatching time and in advanced stages of the breeding cycle.

Before proceeding with the correlation analysis or ANCOVA, I checked whether variables had normal distribution. If the departure from normality was significant, the data were transformed using the angular transformation (for percentages) or (for other variables) an optimal transformation formula was sought with the Box-Cox algorithm (Sokal & Rohlf 1995) to satisfy requirements of Kolmogorov-Smirnov test ($P > 0.1$) for normal distribution. Some 95% confidence intervals presented in section "Results" are not symmetrical because they were calculated with transformed data or with the use of bootstrap simulations (see above). All p -values in significance tests are two-tailed. Experiments with the Polecat and the Harrier will be referred to as, respectively, PO- and HA-experiments.

3. Results

3.1. Description of antipredator behaviour

Only females reacted towards the presented models of predators. Nest defence behaviour consisted mainly of calls and flights.

Calls. Disturbed females gave two kinds of call: a short "check" and a longer, louder and more conspicuous (at least to humans) "trr".

Flights. Females often moved from one post to another, always round the model and not over it. A movement longer than 0.5 m was defined as a "flight".

In experiments with both models call rates correlated with flight rates (in the case of harrier the correlation was marginally significant). In HA experiments, the frequency of flights increased significantly as females approached closer the predator (Table 1; see also below).

3.2. Influence of offspring age, offspring number and time of season

In the presence of both predators, call rates increased with the age of offspring. The increase in the frequency of flights was significant only in HA experiments. The decrease in minimum distances was not significant either in the HA or the PO experiments (Table 2, Fig. 1).

Generally, both hypotheses predict an increase in nest defence. Therefore it is difficult to discriminate between them using correlation analysis. However, the exact pattern of increase is different. In the vulnerability model, we should expect

a rapid increase in nest defence just after hatching, followed by a period of a less sharp growth. In contrast, the offspring value model requires a gradual increase in nest defence, without the threshold around hatching time. These differences could be expressed in a quantitative form allowing to test which hypothesis better fits empirical data. If an increase (A) in reaction level observed around hatching will be stronger than an increase (B) observed in advanced stages of the nestling period (i.e. $A-B > 0$), the vulnerability hypothesis should be preferred. Otherwise (i.e. $A-B \leq 0$), the offspring value hypothesis would be supported. The value of A was calculated as a

Table 1. Relationships between the three measures of intensity of nest defence. Coefficients of the product-moment correlation given in the upper right part of the table refer to the HA experiments ($n=45$) and those in the lower left part to the PO experiments ($n = 45$).

	Call rate			Flight rate			Min. distance		
	r	n	p	r	n	p	r	n	p
Call rate				0.287	45	0.056	-0.084	32	0.648
Flight rate	0.622	45	0.001				-0.581	32	0.001
Min. distance	-0.196	35	0.259	-0.130	35	0.475			

Table 2. Relationships between measures of defence intensity (call rate, flight rate and minimum distance from the predator) and factors hypothesised to influence it (offspring age, offspring number and breeding season advancing) in experiments with the Polecat and the Harrier. Partial product-moment correlation coefficients (see legend) are given with 95% bootstrap percentile confidence limits.

	Polecat				Harrier			
	partial r	lower/upper c.l.	n	p	partial r	lower/upper c.l.	n	p
Offspring age vs.								
Call rate ^{b, c}	0.510	0.282/0.670	45	0.001	0.576	0.358/0.752	45	0.001
Flight rate ^{b, c}	0.171	-0.117/0.451	45	0.261	0.295	0.006/0.544	45	0.049
Min. dist. ^{b, c}	-0.112	-0.427/0.196	35	0.522	-0.175	-0.482/0.144	32	0.338
Number vs.								
Call rate ^{a, c}	0.038	-0.200/0.286	45	0.804	0.198	-0.126/0.468	45	0.192
Flight rate ^{a, c}	0.112	-0.147/0.378	45	0.464	0.160	-0.084/0.392	45	0.294
Min. dist. ^{a, c}	0.109	-0.219/0.327	35	0.532	-0.031	-0.361/0.235	32	0.866
Season vs.								
Call rate ^{a, b}	-0.250	-0.478/0.016	45	0.098	-0.218	-0.439/0.059	45	0.150
Flight rate ^{a, b}	-0.055	-0.368/0.245	45	0.720	-0.155	-0.404/0.139	45	0.309
Min. dist. ^{a, b}	0.099	-0.296/0.354	35	0.571	-0.117	-0.432/0.197	32	0.524

^a offspring age held constant

^b offspring number held constant

^c season advancing held constant

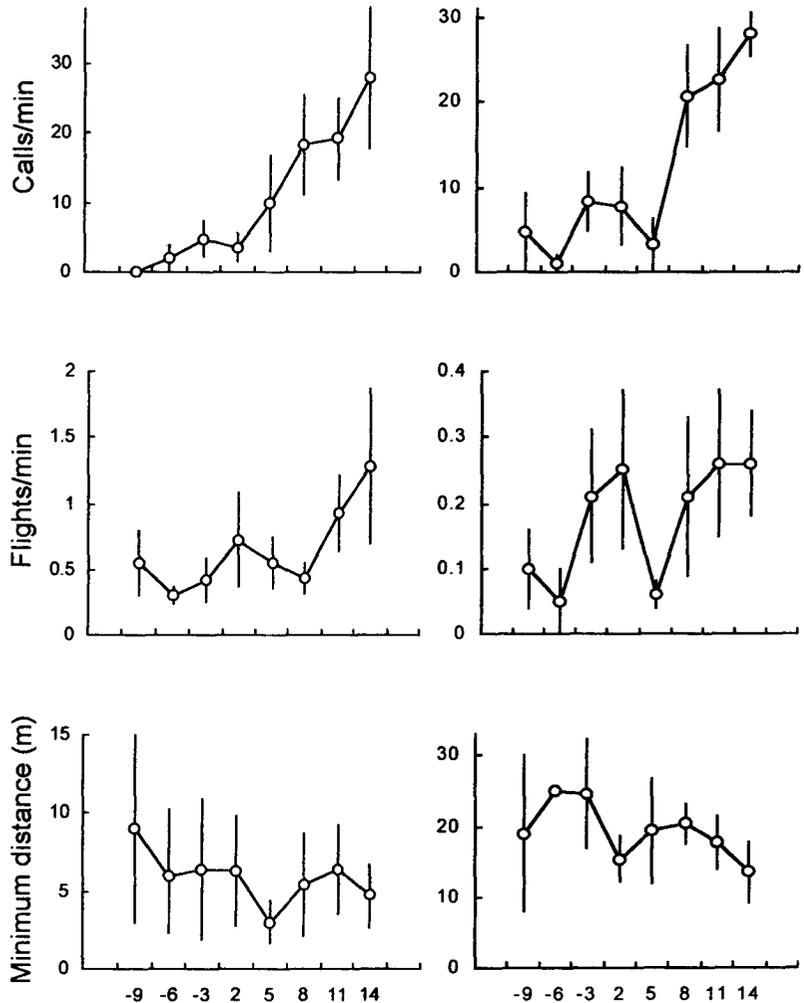


Fig. 1. Influence of offspring age (in days; negative values refer to the incubation period) on nest defence level by females Aquatic Warbler exposed to the Polecat (left column) and Harrier. Three-day averages with standard deviations are shown.

difference between median intensity of nest defence during four days preceding hatching and four following days. B was calculated as a difference between median level of defence by parents having 8–11 versus 12–15 day nestlings. Since the probability distribution of A–B was not known, I bootstrapped this value (5 000 iterations). Results are shown in Table 3. Confidence intervals for A–B overlapping zero suggest that the increase in nest defence was similar around hatching and in advanced stages of the nestling period. Thus the offspring value hypothesis seemed to be better supported by the data.

The signs of correlation coefficients suggest a slightly stronger investment in larger clutches/broods and a weak seasonal decrease in the intensity of

nest defence. However, these trends were not significant (Table 2).

3.3. Influence of predator species

Since most females were tested with both predator models, when comparing their reaction to each predator type, a test for matched pairs was employed. I compared the reaction of individuals presented with each predator controlling for the effect of offspring age (an ANCOVA model with individual females and predator type as factors and offspring age as a covariate).

During PO experiments females approached the predator more closely and were more mobile

than during HA experiments whereas calling rates were similar (Fig. 1 and 2). However, in the presence of the Polecat females uttered significantly more “trrs” than in the presence of the Harrier (Fig. 2).

4. Discussion

4.1. Influence of offspring age

The level of nest defence tended to increase through the breeding cycle and the offspring value hypothesis better explained the pattern of growth in parental reaction than the vulnerability hypothesis (Greig-Smith 1980, Onnebrink & Curio 1991, Meilvang et al. 1997).

The strongest correlation with the breeding stage was found for call rates, the least risky element of defence behaviour. Flight rates and minimum distances, that seem to be better indices of undertaken risk, did not change significantly or their increase/decrease was less pronounced. This may be a feature of parental behaviour in species with uniparental care, where the potential cost of nest defence is greater than in biparental species, since the death or injury of the parent always dramatically reduces the probability of survival of the current offspring (Montgomerie & Weatherhead 1988, see also Lazarus & Inglis 1986 for a discussion of “present costs” of nest defence).

4.2. Influence of offspring number and season advancing

The offspring number did not influence the level of defence. This could support the hypothesis that

Table 3. The 95% bootstrap percentile confidence intervals for the difference between A and B value (see text for details) in measures of nest defence, which showed a significant increase with age of the offspring.

	Harrier lower/upper c.l.	Polecat lower/upper c.l.
Call rate	– 20.0/8.9	– 32/11.3
Flight rate	– 0.2/0.3	

in species with uniparental care such a relationship need not be observed (Lazarus & Inglis 1986, Montgomerie & Weatherhead 1988). However, also in many biparental species did clutch/brood size not affect parental investment in nest defence (e.g., Rytönen et al. 1995, Vinuela et al. 1996). The results seem to support the idea that the given clutch size is optimal for the parent because it represents a certain proportion of lifetime reproduction (Montgomerie & Weatherhead 1988, Clutton-Brock 1991). The experimental manipulation of brood size could be the only way to advance research of this problem (e.g., Wiklund 1990, Rytönen et al. 1995).

The results of this study run counter to the prediction that diminishing reneesting potential should enhance nest defence through the season (see also Rytönen et al. 1995, Halupka & Halupka 1997). The effect of this factor, however, may have been balanced by the decrease in offspring value due to diminishing survival prospects (Wiklund 1990, Hakkarainen & Korpimäki 1994). As the season progressed, the offspring mortality increased as a result of adverse weather, decline in food abundance and insufficient food delivery: in early season significantly greater proportion of laid eggs yield fledglings, compared to that in late season (Dyrce & Zdunek 1993b).

4.3. Influence of predator species

Nest defence behaviour evoked by the Polecat and the Harrier differed both in structure and intensity, demonstrating that the antipredator behaviour of Aquatic Warblers is predator-specific. The Polecat was approached much closer (minimum distance is considered as the best indicator of the undertaken risk, e.g., Curio 1975) and distracted more vigorously (frequency of flights) than the Harrier. This may reflect differences in the threat that these predators pose to adult warblers (see Methods). Overall rates of calls, the least risky element of the behaviour, did not differ between models. However, there was a significant difference in the proportion of two calls used. The long and conspicuous “trrs” were uttered more often in the presence of Polecat, which could depredate the nest but was relatively “safe” for mature birds, while the short and difficult to localise “checks”

to distract the Harrier, which could pursue and kill the nest defender. Females may have adjusted the kind of call (sound of a particular frequency, pitch and timbre) so as it was best perceived by the given type of predator (cf. East 1981, Gochfeld 1984). It is also possible that the two calls play different roles. Greig-Smith (1980) in Stonechats *Saxicola rubetra* and East (1981) in Robins *Eritacus rubecula* found that one call (high-pitched and with a narrow frequency range) functioned as a warning signal and caused nestlings to stop begging, whereas another call (that covered a wide range of frequencies and was combined with flights and a closer approach to the predator) was used to distract an intruder from the nest. There are some similarities between characteristics of the two call-types of Stonechats and Robins on the one hand, and "checks" and "trrs" of Aquatic Warblers on the other. This resemblance may suggest that they also have similar functions. Harriers use acoustical cues while hunting (Rice 1982), therefore uttering calls ("checks") that silence the young would be adaptive for the female. Such a strategy seems to be less useful in the case of smell-guided predators.

4.4. Concluding remarks

The type of predator well explained variation in nest defence by Aquatic Warblers. Other factors (offspring age and number, stage of the breeding season) were much worse predictors. Only the offspring age correlated significantly with the response of females: they increased alarm calling rate, but apparently did not vary their flight rate and minimum distance, components of behaviour assumed to be better correlates of risk-taking. Such results cannot be explained as a side-effect of small sample size or insufficient statistical power of tests. Confidence intervals of correlation coefficients (Table 2) considerably overlapping both the positive and negative values close to zero, suggest that the null hypotheses were indeed more likely than their alternatives (Steidl et al. 1997). I suggest that most of findings presented in this study could be interpreted as a consequence of uniparental care. However, as there have been no other studies of nest defence by altricial species with such a type of parental care, we should wait for more data to make more firm generalisations.

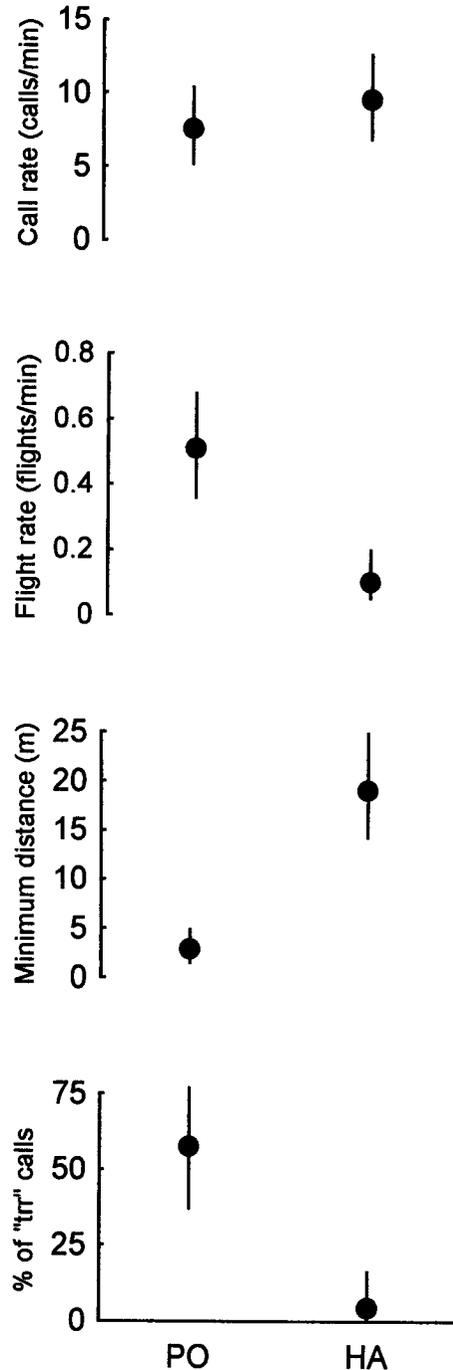


Fig. 2. Differences in the reaction of females towards the Polecat and the Harrier. Averages and their 95% confidence limits are shown. Statistics refer to the ANCOVA: call rate: $F_{1,37} = 1.02$, $p = 0.319$; flight rate: $F_{1,37} = 21.40$, $p < 0.001$; minimum distance: $F_{1,19} = 51.00$, $p < 0.001$; percentage of "trr" calls: $F_{1,21} = 20.05$, $p = 0.0002$.

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Selostus: Sarakerttusen pesän puolluskäyttäytyminen suhteessa pesyeen ikään, pesyekokoon, pesimäkauden vaiheeseen ja petolajiin

Kirjoittaja tutki pesän puollustuksen voimakkuutta eri tilanteissa sarakerttusella Koillis-Puolassa. Työn tarkoitus oli testata aiemmin esitettyjä hypoteesejä pesän puollustusintensiteetin vaihtelusta pesyeen iän, pesyekoon ja pesimäkauden vaiheen mukaan sekä selvittää erilaisten petotyyppien merkitystä tässä vaihtelussa. Sarakerttusella vain naaras osallistuu pesyeen ruokintaan ja puollustamiseen. Kirjoittaja järjesti kokeen, missä eri pesien naaraille näytettiin kahta vaihtoehtoista petomallia, täytettyä sinisuohaukkaa tai hilleriä. Molemmat lajit ovat alueella sarakerttusen luontaisia petoja. Pesän puollustuksen intensiteettiä mitattiin varoitusäänien määrällä aikayksikköä kohti, minimietäisyydellä petomalliin ja pedon ympärillä tehtyjen siirtymisten määrällä. Pesän puollustuksen voimakkuus kasvoi pesimäkauden edessä. Kirjoittaja osoitti, että havaittu voimakkuuden lisäys oli selitettävissä paremmin jälkeläisten arvo -hypoteesin (offspring value hypothesis) kuin jälkeläisten haavoittuvuus -hypoteesin (offspring vulnerability hypothesis) avulla. Jälkeläisten arvo -hypoteesin mukaan vanhemmat jälkeläiset ovat arvokkaampia emon kannalta kuin nuoret jälkeläiset, koska emo on panostanut enemmän aikaa ja resursseja vanhempiin jälkeläisiinsä, mikä vuoksi vanhempia jälkeläisiä kannattaa puollustaa voimakkaammin (suuremmalla riskillä). Jälkeläisten määrä ja pesimäkauden eteneminen sinänsä eivät vaikuttaneet pesän puollustuksen tasoon. Petolajien välillä oli kuitenkin selkeä ero naaraiden käyttäytymisessä. Odotuksen mukaisesti naaraat ottivat suuremman riskin (liikkuivat enemmän lähempänä petomallia) hillerin ollessa petomalli kuin sinisuohaukkan kanssa. Naaraat näyttivät käyttävän eri varoitusääntä hillerin kuin sinisuohaukan läsnäollessa.

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