

# Does fresh vegetation protect avian nests from ectoparasites? An experiment with tree swallows

Russell D. Dawson

**Abstract:** Some species of birds incorporate fresh green vegetation into their nests. The adaptive significance of this behaviour, however, is unclear. The “nest protection hypothesis” suggests that volatile chemicals contained in green plants reduce populations of nest-dwelling ectoparasites. I tested this hypothesis with tree swallows, *Tachycineta bicolor* (Vieillot, 1808), a species that has large infestations of ectoparasites in its nests. I experimentally added green leaves of yarrow (*Achillea millefolium* L.) to nests and compared these nests to control nests. My results showed that nests with yarrow had significantly higher levels of infestation by fleas, and yarrow had no effect on the number of blow flies detected. There was no effect of yarrow on condition of parents, size of offspring, or the probability of nests fledging at least one young. I did, however, find that second-year (SY) females with yarrow added to their nests hatched significantly more eggs than control SY females. In addition, pairs with yarrow added to their nest were significantly less likely to suffer hatching failure and (or) brood reduction. These beneficial effects of yarrow cannot be explained by reductions in numbers of fleas or blow flies, and I suggest that these results may be due to reductions in numbers of other types of parasites not quantified in my study, such as flying insects or the diseases that they may vector. I discuss my findings for swallows in the context of results from previous studies of other species that habitually use green plant material such as yarrow in their nests.

**Résumé :** Quelques espèces d'oiseaux incorporent de la végétation verte fraîche dans leurs nids. La fonction d'adaptation d'un tel comportement reste, cependant, incertaine. L'«hypothèse de protection du nid» veut que les produits chimiques volatils contenus dans les plantes vertes réduisent les populations d'ectoparasites dans le nid. L'hypothèse a pu être vérifiée chez des hirondelles bicolores, *Tachycineta bicolor* (Vieillot, 1808), des oiseaux qui possèdent de fortes infestations d'ectoparasites dans leur nid. Des nids portant des feuilles vertes de l'achillée millefeuille ont été comparés à des nids témoins. Les nids avec de l'achillée ont des taux d'infestations de puces significativement plus élevés, alors que l'achillée reste sans effet sur les nombres de mouches de la viande observées. L'achillée est aussi sans effet sur la condition physique des parents, la taille des petits et la probabilité qu'au moins un petit prenne son envol du nid. Cependant, dans les nids munis d'achillée des femelles de seconde année (SY), l'éclosion des oeufs est plus importante que dans les nids de femelles SY témoins. De plus, il y a une probabilité plus faible d'éclosions ratées et (ou) de réduction des couvées chez les couples possédant un nid muni d'achillée. Ces effets bénéfiques de l'achillée ne peuvent s'expliquer par une réduction de puces ou de mouches de la viande; ces résultats peuvent être dus à la réduction d'autres parasites non dénombrés dans cette étude, tels que les insectes volants et les maladies qu'ils peuvent transmettre. Les résultats obtenus chez les hirondelles sont examinés dans le contexte d'études antérieures sur d'autres espèces qui utilisent communément du matériel végétal vert, tel que de l'achillée, dans la construction de leurs nids.

[Traduit par la Rédaction]

## Introduction

Many species of birds incorporate fresh green vegetation into the substrate of their nests. However, the functional significance underlying this behaviour is unclear. Of six possible hypotheses summarized by Clark (1991) to explain this behaviour, the “nest protection hypothesis” has received the most attention (Wimberger 1984; Clark and Mason 1988). All plants contain secondary metabolites that are used as a defence against disease and herbivory (Clark and Mason

1988); the nest protection hypothesis suggests that birds exploit these insecticidal properties by incorporating into their nests certain plant species that emit large amounts of volatile chemicals. Therefore, green vegetation is used adaptively by birds to reduce parasites and pathogens within the nest environment. Because population sizes of nest-dwelling ectoparasites are thought to increase at an individual nest site over successive breeding episodes, Wimberger (1984) provided support for the nest protection hypothesis by showing that among Falconiformes, the probability of reusing a nest site correlated with the probability of incorporating green vegetation in nests. Similarly, Clark and Mason (1985) reviewed literature on life histories of passerines and found that greenery was more often associated with hole nesters that reused nest sites than with cup nesters that rarely reused nest sites.

Much of the research on the function of green plant material in nests has used the European starling (*Sturnus vul-*

Received 22 November 2003. Accepted 8 June 2004.  
Published on the NRC Research Press Web site at  
<http://cjz.nrc.ca> on 20 August 2004.

**R.D. Dawson.** Ecosystem Science and Management Program,  
University of Northern British Columbia, 3333 University  
Way, Prince George, BC V2N 4Z9, Canada (e-mail:  
[dawsonr@unbc.ca](mailto:dawsonr@unbc.ca)).

*garis* L., 1758) as a model. The results of these studies, however, have not universally supported the nest protection hypothesis and, indeed, the function of green plants in nests remains equivocal. For example, Clark and Mason (1988) showed that greenery in nests of starlings significantly reduced mite populations, whereas Gwinner et al. (2000) discounted these findings because starlings bring greenery to nests only until eggs are laid (Clark and Mason 1985) and not during brood rearing, when build-up of ectoparasites may be particularly deleterious. In addition, there is evidence that green plants may be important for male starlings to attract mates (e.g., Fauth et al. 1991; Eens et al. 1993; Gwinner 1997). To disentangle whether the behaviour of bringing greenery to a nest has evolved for antiparasite or courtship purposes in starlings, it may be informative to perform experiments on other species whose nests are highly infested by ectoparasites but that do not bring green nesting material to their nests. By using such a study system, the potentially confounding role of green plant material in courtship is removed.

In my study area in north central British Columbia, Canada, starlings are known to bring sprigs of yarrow (*Achillea millefolium* L.) to their nests prior to and during egg laying (unpublished data). In contrast, tree swallows (*Tachycineta bicolor* (Vieillot, 1808)) breeding in the same area (and the same nest boxes) do not show this behaviour and instead construct their nests entirely from dead grasses and feathers (see also Robertson et al. 1992). Both species have high levels of parasite infestation (Clark 1991; Robertson et al. 1992; Dawson 2004). Because greenery does not appear to play a role in courtship of tree swallows, this species may be appropriate for testing the nest protection hypothesis because courtship rituals do not confound results. Moreover, if the nest protection hypothesis is supported, this leads to the interesting question of why bringing greenery to nests has not evolved in species such as tree swallows. I experimentally added yarrow leaves to a sample of tree swallow nests during early incubation as well as the nestling period and compared parasite loads and reproductive success of these nests with those of a group of control nests. I also used a second control group of nests to which leaves of brome grass (*Bromus inermis* Leyss.) were added (hereinafter, the brome group). Although most tree swallows in my study area used dead brome grass as nesting material, live green brome is not selected by either swallows or starlings as nesting material, perhaps because it does not contain large amounts of volatile chemicals compared with plants such as yarrow (see Clark and Mason 1985). Thus, this second control group helps to differentiate whether the addition of green plant material per se, or the addition of green plants with high levels of volatile chemicals, is responsible for any effects detected.

## Materials and methods

I studied breeding tree swallows from May to August 2001 near Vanderhoof, British Columbia, Canada (54°N, 124°W). Tree swallows arrived in my study site during early May and began constructing nests and laying eggs by mid-to late May. The study site is approximately 800 km<sup>2</sup> and is composed of open agricultural areas mixed with small

patches of coniferous and deciduous trees and small wetlands. Tree swallows bred in nest boxes mounted approximately 3 m above the ground on electrical poles. Nest boxes were located about 800 m apart and 5–10 m from roads. All boxes used in this study had several centimetres of wood shavings in the bottom, and all boxes were constructed just prior to the 2001 breeding season; therefore, residual parasite infestations from past breeding events did not bias my data set.

Beginning in early May, I visited each nest box every 3–4 days until a clutch had been initiated. Nests were monitored until clutches were completed, and I then sequentially allocated nests to one of three treatments: control, yarrow, or brome. At 4–5 days after clutch completion, I visited nests assigned to the yarrow group and harvested approximately 3 g of fresh yarrow from within 20 m of the nest. I then loosely wove the fresh yarrow into the nest cup. Nests assigned to the brome group were treated in an identical manner except that leaves of brome grass were woven into the nest cup. At control nests, I handled nesting material in a similar fashion to the brome and yarrow treatments but did not add any extra vegetation.

I visited boxes every 1–2 days near the predicted hatching date to determine when the first nestling emerged from its egg and the number of eggs that hatched. As soon as all eggs had hatched, I captured adults in the nest box using a swing-door trap. Each bird was banded and weighed (nearest 0.25 g), and the length of the ninth primary flight feather was measured (nearest 0.5 mm). I used plumage colouration to classify females as being either in their second year (SY) or older (after second year, ASY) (details in Robertson et al. 1992). When nestlings were 6 days old, I again added yarrow or brome to nests and handled nesting material at control nests. In contrast to methods used during incubation, during this visit I added approximately twice the amount of fresh plant material (6 g) to yarrow and brome nests. In total, the amount of green material added to nests in my experiment far exceeded the amount of yarrow added by starlings to their nests in my study area, which add only several small sprigs. Each nestling was also weighed (nearest 0.25 g) at 6 days of age. Nestlings were banded with standard aluminum leg bands when they were 12 days old, at which time I again weighed them and measured the length of their ninth primary flight feather (nearest 1 mm). For all analyses of mass and length of the ninth primary, I calculated the means for each nest and used these values in statistical tests.

Nests were not visited again until 23–24 days post hatch, by which time nestlings had fledged. All nesting material was carefully removed from each box and stored in bags at room temperature for 14 days. This allowed larval blow flies to complete pupation and adults to emerge. Nests were then dried in an oven at 80 °C overnight and nesting material was carefully teased apart to count all adult fleas and pupal cases of blow flies. To avoid any potential biases associated with nests that failed before fledging, I quantified ectoparasites only at nests where offspring had survived to at least 12 days old. Although I present means for raw data in the results, data on numbers of fleas were log transformed prior to analysis to meet assumptions of normality and homogeneity of variances.

**Table 1.** Comparison of control nests of tree swallows (*Tachycineta bicolor*) with those to which fresh vegetation (yarrow or brome grass) was added during the incubation and nestling periods.

Variable	Treatment		
	Yarrow	Brome	Control
Clutch size	5.7±0.2 (n = 10)	5.8±0.2 (n = 8)	5.9±0.2 (n = 13)
Clutch initiation date <sup>a</sup>	159.6±2.5 (n = 14)	159.4±2.6 (n = 13)	154.5±2.8 (n = 11)
Fleas (number)	719.6±161.7 (n = 8)	233.4±181.8 (n = 6)	40.1±208.6 (n = 5)
<i>Protocalliphora</i> spp. (number)	57.0±16.0 (n = 8)	76.2±18.5 (n = 6)	56.0±20.3 (n = 5)
Male parents, mass (g)	19.3±0.3 (n = 13)	19.7±0.3 (n = 9)	20.2±0.3 (n = 9)
Female parents, mass (g)	19.4±0.3 (n = 14)	19.7±0.3 (n = 11)	19.9±0.4 (n = 9)
Nestlings, mass at 6 days (g)	12.4±0.3 (n = 12)	12.2±0.4 (n = 7)	13.2±0.5 (n = 6)
Nestlings, mass at 12 days (g)	22.3±0.4 (n = 7)	22.7±0.5 (n = 5)	22.4±0.4 (n = 5)
Nestlings, length of 9th primary flight feather at 12 days (mm)	25.8±1.0 (n = 7)	24.7±1.1 (n = 5)	27.4±1.3 (n = 4)
Number fledged	4.7±0.3 (n = 8)	5.0±0.4 (n = 6)	4.9±0.4 (n = 5)

**Note:** Means (±1 SE) are presented; except for number of *Protocalliphora* spp. and mass of male parents, means were calculated after controlling for covariates in models (see Results). Except for number of fleas ( $P = 0.09$ ), differences among treatments did not approach significance (all  $P$  values >0.10).

<sup>a</sup>1 = 1 January.

### Data analysis

Nests were manipulated after clutch completion, so I first tested whether there were any preexisting differences in date of clutch initiation or clutch size among treatments. The test for initiation date used analysis of covariance (ANCOVA) with age, ninth primary length, and mass of the female parent, and ninth primary length and mass of the male parent, (hereafter parental attributes) as possible explanatory variables. The analysis of clutch size was similar, except that clutch initiation date was included as an additional covariate. I then compared ectoparasite loads among treatments using ANCOVA with hatching date and brood size at day 12 as potential covariates. To investigate whether the addition of fresh plant material to nests had consequences for the body condition of parents, I tested whether mass of parents at the conclusion of incubation differed among treatments. These analyses used ninth primary length and clutch initiation date as potential covariates. The analyses for female parents also included age as a factor. I used ANCOVA to test whether treatment affected number of eggs hatched, mass of offspring at 6 and 12 days of age, length of ninth primary of nestlings at age 12 days, and the number of offspring fledged. In addition to treatment, all of these analyses included parental attributes and hatching date in the models. The analysis for number hatched also included clutch size as an additional covariate, while analyses for mass and length of ninth primary of nestlings also included brood size as a covariate. The analysis of number of young fledged used number hatched as an additional covariate. For each of the above analyses, I first ran models with all factors and covariates plus first-order interactions. I then used a stepwise backward procedure to eliminate all nonsignificant interactions and terms. Final models always included the variable of interest, vegetation treatment.

I used contingency tables to test whether there were differences among treatments in overall success of parents in raising offspring. In one analysis, I considered all nests that fledged at least one young to be successful and those where no young were fledged to be unsuccessful. In a second analysis, I divided nests into two groups: one in which parents successfully hatched all of their eggs and fledged all of their

young, and one that consisted of nests that showed at least some degree of failure, either in hatching eggs or raising offspring. This latter group therefore consisted of those nests experiencing either partial or total hatching failure and (or) nestling mortality.

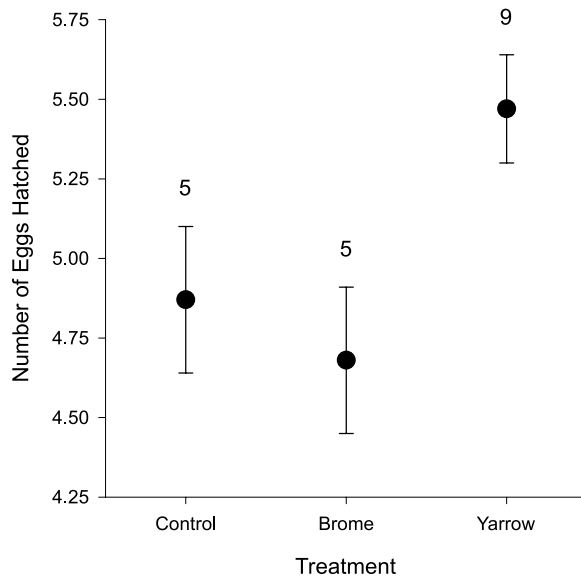
Statistical analyses were performed using SPSS (Norusis 1993). All tests are two-tailed, and means (±1 SE) are presented. Sample sizes in some analyses were small, so to increase power I considered results significant at the  $P < 0.10$  level.

### Results

A total of 39 nests were used in this study, with 14 nests allocated to yarrow treatment, 13 to brome treatment, and 12 to the control group. There were no significant differences in clutch size among treatments ( $F_{[2,26]} = 0.09$ ,  $P = 0.92$ ; Table 1); however, young (SY) females laid significantly fewer eggs than did older (ASY) females ( $F_{[1,26]} = 5.40$ ,  $P = 0.03$ ) and pairs breeding later in the season also laid fewer eggs ( $F_{[1,26]} = 7.28$ ,  $P = 0.01$ ). My analyses also showed that there were no differences in clutch initiation date among treatments ( $F_{[2,35]} = 1.16$ ,  $P = 0.33$ ; Table 1). Collectively, these results indicate that there were no differences among nests prior to the manipulations.

I detected one species of bird flea (*Ceratophyllus idius* Jordan and Rothschild, 1920) and at least four species of blow fly (*Protocalliphora braueri* Hendel, 1901; *P. occidentalis* Whitworth, 2003; *P. bennetti* Whitworth, 2002; and *P. rugosa* Whitworth, 2002) in nests of tree swallows. The number of fleas in nests where young survived to 12 days of age declined as hatching dates occurred later in the season ( $F_{[1,15]} = 6.31$ ,  $P = 0.02$ ). There were also differences among treatments in the number of fleas detected ( $F_{[2,15]} = 2.79$ ,  $P = 0.09$ ; Table 1); however, these results are opposite to those predicted in that nests with yarrow had more fleas than did control nests. I detected no significant differences among treatments in the number of blow flies detected in nests ( $F_{[2,16]} = 0.38$ ,  $P = 0.69$ ). The numbers of fleas and blow flies were not correlated within nests ( $r = 0.32$ ,  $n = 19$ ,  $P = 0.18$ ).

**Fig. 1.** Mean ( $\pm$ SE) number of eggs hatched, after controlling for variation in clutch size, by second-year female tree swallows (*Tachycineta bicolor*) in three nest vegetation treatments. Sample sizes indicated above error bars refer to number of nests.

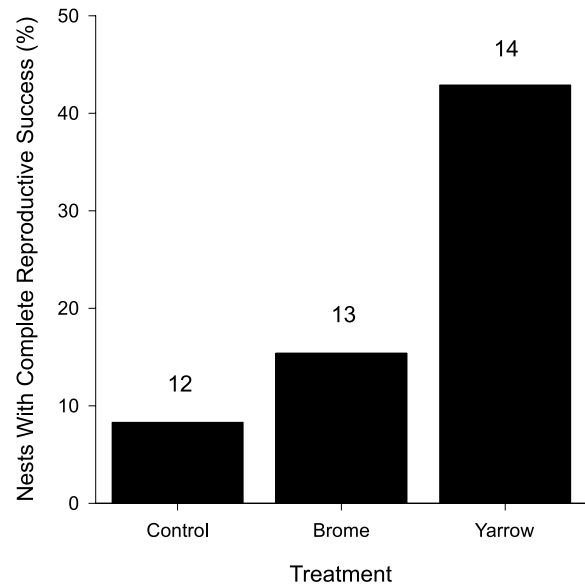


The addition of fresh vegetation to nests during incubation had no significant effects on mass of male parents ( $F_{[2,28]} = 2.30$ ,  $P = 0.12$ ) and, if anything, males that had yarrow added to their nests also had the lowest body mass (Table 1). For female parents, there was evidence that those with a larger body, estimated from the length of the ninth primary flight feather, were also heavier ( $F_{[1,30]} = 9.02$ ,  $P < 0.01$ ), but there were no differences in mass of females among treatments ( $F_{[2,30]} = 0.61$ ,  $P = 0.55$ ; Table 1).

My analysis of the number of eggs hatched included several parental attributes as potential covariates. Because I trapped adults only once eggs had hatched, these analyses were limited to nests in which at least one egg had hatched. When these data were analyzed, however, I found a significant interaction between treatment and age of the female parent ( $F_{[2,24]} = 6.21$ ,  $P < 0.01$ ), so these data were then analyzed separately for nests with older (ASY) and younger (SY) females. Not surprisingly, the number of eggs hatched by ASY females increased with clutch size ( $F_{[1,8]} = 38.89$ ,  $P < 0.001$ ), but there was no significant difference in number hatched among treatments ( $F_{[2,8]} = 3.01$ ,  $P = 0.11$ ). The number of eggs hatched by SY females also increased with clutch size ( $F_{[1,15]} = 22.06$ ,  $P < 0.001$ ); however, there was a significant effect of treatment on number hatched ( $F_{[2,15]} = 4.48$ ,  $P = 0.03$ ; Fig. 1). A post hoc Tukey HSD test revealed that after controlling for the effects of clutch size, birds with yarrow in their nests hatched significantly more young than did those with brome ( $P = 0.03$ ), but that yarrow nests did not differ from control nests, nor did control and brome nests differ ( $P > 0.05$  in both cases).

The mean mass of nestlings at 6 days old was positively related to brood size ( $F_{[1,20]} = 4.52$ ,  $P = 0.05$ ), and increased with mass of male parents ( $F_{[1,20]} = 4.15$ ,  $P = 0.06$ ), but was not different among treatments ( $F_{[2,20]} = 1.27$ ,  $P = 0.30$ ). At 12 days of age, mass of nestlings was also similar among treatments ( $F_{[2,13]} = 0.29$ ,  $P = 0.75$ ), and mass of nestlings was positively related to the length of their male parent's

**Fig. 2.** Percentage of nests of tree swallows in three nest vegetation treatments that had 100% hatching and fledging success. Sample sizes in each category are indicated above bars and refer to number of nests.



ninth primary ( $F_{[1,13]} = 13.52$ ,  $P < 0.01$ ). Results for length of the ninth primary at 12 days showed no effect of treatment ( $F_{[2,11]} = 1.27$ ,  $P = 0.32$ ), but length of primaries was negatively related to the mass of male parents ( $F_{[1,11]} = 3.19$ ,  $P = 0.03$ ). In addition, primaries of nestlings with ASY female parents were longer than those of nestlings with SY female parents ( $F_{[1,11]} = 7.66$ ,  $P = 0.02$ ). Among nests that fledged at least one young, the number fledged increased with the number of chicks hatched ( $F_{[2,15]} = 23.78$ ,  $P < 0.001$ ), but treatment was not significant ( $F_{[2,15]} = 0.20$ ,  $P = 0.82$ ; Table 1).

There was no difference among treatments in the probability that nests would fledge at least one young ( $\chi^2 = 0.67$ ,  $df = 2$ ,  $P = 0.72$ ); however, there was evidence that birds that had yarrow added to their nests were less likely to experience hatching failure or nestling mortality; i.e., birds with yarrow were more likely to fledge a number of young equal to their clutch size ( $\chi^2 = 4.99$ ,  $df = 2$ ,  $P = 0.08$ ; Fig. 2).

## Discussion

The experimental addition of yarrow to the nesting material of tree swallows did not reduce levels of ectoparasite infestation. Although sample sizes were small, I detected no significant difference in the number of blow flies among treatments and, contrary to expectation, nests with yarrow had significantly higher numbers of fleas than did control nests (Table 1). Lafuma et al. (2001) cited unpublished data suggesting that nests of blue tits (*Parus caeruleus* L.) with green plants had high levels of infestation by *Protocalliphora* spp., and Rodgers et al. (1988) showed that dermestid beetles of wood storks (*Mycteria americana* L., 1758) were not repelled by green plants in nests. The results of these studies are in contrast to those of Clark and Mason (1985, 1988; see also Clark 1991), who showed that experimental addition of green plant material to nests of starlings signifi-

cantly reduced levels of infestation. The preferred plants of starlings, wild carrot (*Daucus carota* L.) and flea bane (*Erigeron philadelphicus* L.), seemed to have little effect on mortality of adult mites but instead reduced emergence of feeding instars (Clark and Mason 1985). Fauth et al. (1991), who failed to show significant effects of greenery on ectoparasite loads in starling nests, suggested that Clark and Mason's (1988) results may have been due to their protocol of adding greenery after hatching (which starlings normally do not do) and in quantities greater than starlings usually bring to nests. However, I failed to show any beneficial effects of adding yarrow both before and after hatching in tree swallows. The inconsistency in the results of the above studies may be because adding green plants with insecticidal properties to nests may have differential effects on the parasitoids and predators of the nest-dwelling ectoparasites. For example, Stathers et al. (2002) found that populations of insect pests in some stored crops were higher when treated with insecticides, and they attributed these differences to reductions in populations of predators of the pests. If this is true, any effects of greenery on ectoparasites may be masked because of reductions in populations of parasitoids and predators, resulting in no detectable effects on ectoparasite numbers, or even increased numbers, when nests have green plants added to them.

Studies that have examined the effects of green plant material on ectoparasites in nests have focussed their attention on nestlings, while possible effects on adult parents have generally been ignored. Parent birds with nests infested with ectoparasites may need to spend more time performing antiparasite behaviour at the expense of other activities such as foraging (Christe et al. 1996). One potential benefit of placing green plants in nests prior to the nestling period may be that it allows parents, particularly females, to incubate more efficiently. However, adding yarrow to nests soon after incubation began did not significantly influence the body mass of either sex of parent tree swallows (Table 1).

There is abundant evidence that ectoparasites can have significant effects on growth and survival of nestling birds (review in Møller 1997). I detected no benefits of yarrow on the mass or feather length of offspring when they were either 6 or 12 days old (Table 1). These results are not surprising, given the inability of yarrow to reduce parasite loads in nests. Clark and Mason (1988) also showed no significant effect of addition of greenery on mass or feather growth of nestling starlings, but haemoglobin levels of nestlings were higher in nests where greenery was added. Because haemoglobin levels are indicative of oxygen carrying capacity, Clark and Mason (1988) suggested that lower levels might have implications for survival of chicks after they leave the nest. However, Fauth et al. (1991) found no effect of greenery in nests on post-fledging survival of starlings. Gwinner et al. (2000) also found no effect of green plants on fledging success or cell-mediated immune responses of starlings but, interestingly, found chicks to be in significantly better condition and more likely to recruit, even though there was no reduction in ectoparasite loads when green plants were added to nests. Studies that have failed to find significant effects of greenery on ectoparasite loads, my own included, have not quantified the entire fauna of nests. For example, flying insects may be as significant for reproductive success as nest-

dwelling ectoparasites (Wimberger 1984; see below), yet are rarely, if ever, quantified in these types of studies. Lafuma et al. (2001) found in laboratory experiments that mosquitos generally are repelled and less likely to take a blood meal from domestic chicks when aromatic plants are present in their cages.

My study did suggest that yarrow was associated with enhanced reproductive success of tree swallows. Second-year (SY) females had significantly higher hatching success when yarrow was added to their nests (Fig. 1), and there was evidence that birds with yarrow in their nests were less likely to experience reproductive failure, either in hatching eggs or raising offspring (Fig. 2). The mechanism underlying these two results is unclear, but they cannot be a consequence of reduced populations of either fleas or blow flies (Table 1). Similarly, the results for SY females cannot be explained by differences in breeding chronology compared with older females, as hatching date did not contribute significantly to the statistical model in this analysis. One possibility may be that yarrow was effective at repelling parasites that I did not quantify in my study, such as flying insects (Wimberger 1984), to which SY females may be particularly susceptible. Many insects also can be vectors of other disease-causing agents (see Friend and Franson 1999) and so tree swallows with yarrow in their nests may have been less susceptible to these risks. In addition, Clark and Mason (1985) showed that certain plant species retarded the growth of bacteria, although yarrow was the least effective of the plants tested.

While some studies have not demonstrated significant benefits resulting from the use of green plants as nest material by starlings and other birds, the studies by Clark and Mason (1985, 1988) clearly showed that there is potential for greenery to reduce ectoparasite loads. Nonetheless, many researchers have concluded that greenery in nests of starlings does not function solely as a fumigant (Fauth et al. 1991; Gwinner 1997). Eens et al. (1993) showed that when either a male or a female starling was introduced into an aviary, the resident male responded by bringing green nesting material to the nest box. Male starlings often show items, both green plant material and other objects, to females before placing them in the nest box during courtship, which lead Gwinner (1997) to conclude that the primary function of greenery is mate attraction. Green plants in the nests of birds may therefore represent an exaptation (Gould and Vrba 1982), a trait that evolved for one purpose (courtship in the case of starlings) but that has been or could be used for a different purpose (reducing ectoparasite infestations). Similarly, Fauth et al. (1991) suggested that starlings may use odoriferous plants instead of colourful ornaments to attract mates because of low visibility in cavity nests, which is consistent with Clark and Mason's (1985, 1987) findings that starlings select plants based on olfactory cues. Regardless, more experiments are needed to fully address whether green plant material in bird nests is an adaptation against parasitism. Field studies examining the role of flying insects, and the diseases they may vector, are particularly needed.

## Acknowledgements

I thank P.-P. Bitton, M. Dawson, and K. Maitland for help

with field work. I also thank K. Child and A. Pasowisty from BC Hydro for allowing me to erect nest boxes on power poles, T. Whitworth for identifying the *Protocalliphora* spp., and J. Young for advice. Comments from anonymous reviewers were much appreciated. Funding for this research was provided by the Natural Sciences and Engineering Research Council of Canada through a Discovery Grant to R.D.D. Additional support was provided by the University of Northern British Columbia and the Canada Foundation for Innovation.

## References

- Christe, P., Richner H., and Oppliger, A. 1996. Of great tits and fleas: sleep baby sleep. *Anim. Behav.* **52**: 1087–1092.
- Clark, L. 1991. The nest protection hypothesis: the adaptive use of plant secondary compounds by European starlings. *In* Bird-parasite interactions. *Edited by* J.E. Loya and M. Zuk. Oxford University Press, Oxford. pp. 205–221.
- Clark, L., and Mason, J.R. 1985. Use of nest material as insecticidal and anti-pathogenic agents by the European starling. *Oecologia*, **67**: 169–176.
- Clark, L., and Mason, J.R. 1987. Olfactory discrimination of plant volatiles by the European starling. *Anim. Behav.* **35**: 227–235.
- Clark, L., and Mason, J.R. 1988. Effect of biologically active plants used as nest material and the derived benefit to Starling nestlings. *Oecologia*, **77**: 174–180.
- Dawson, R.D. 2004. Efficacy of diatomaceous earth at reducing populations of nest-dwelling ectoparasites. *J. Field Ornithol.* **75**: 232–238.
- Eens, M., Pinxten, R., and Verheyen, R.F. 1993. Function of the song and the song repertoire in the European starling (*Sturnus vulgaris*): an aviary experiment. *Behaviour*, **125**: 51–66.
- Fauth, P.T., Krementz, D.G., and Hines, J.E. 1991. Ectoparasitism and the role of green nesting material in the European Starling. *Oecologia*, **88**: 22–29.
- Friend, M., and Franson, J.C. (Editors). 1999. Field manual of wildlife diseases: general field procedures and diseases of birds. US Geological Survey, Biological Resources Division, Madison, Wisc.
- Gould, S.J., and Vrba, E. 1982. Exaptation — a missing term in the science of form. *Paleobiology*, **8**: 4–15.
- Gwinner, H. 1997. The function of green plants in nests of European starlings (*Sturnus vulgaris*). *Behaviour*, **134**: 337–351.
- Gwinner, H., Oltrogge, M., Trost, L., and Nienaber, U. 2000. Green plants in starling nests: effects on nestlings. *Anim. Behav.* **59**: 301–309.
- Lafuma, L., Lambrechts, M.M., and Raymond, M. 2001. Aromatic plants in bird nests as a protection against blood-sucking flying insects? *Behav. Process.* **56**: 113–120.
- Møller, A.P. 1997. Parasitism and the evolution of host life history. *In* Host-parasite evolution: general principals and avian models. *Edited by* D.H. Clayton and J. Moore. Oxford University Press, Oxford. pp. 105–127.
- Norušis, M.J. 1993. SPSS for Windows. Advanced statistics. Release 6.0 [computer program]. SPSS Inc., Chicago.
- Robertson, R.J., Stuchbury, B.J., and Cohen, R.R. 1992. Tree swallow. *In* The birds of North America. No. 11. *Edited by* A. Poole, P. Stettenheim, and F. Gill. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C. pp. 1–28.
- Rødgers, J.A., Jr., Wenner, A.S., and Schwikert, S.T. 1988. The use and function of green nest material by wood storks. *Wilson Bull.* No. 100. pp. 411–423.
- Stathers, T.E., Mvumi, B.M., and Golob, P. 2002. Field assessment of the efficacy and persistence of diatomaceous earths in protecting stored grain on small-scale farms in Zimbabwe. *Crop Prot.* **21**: 1033–1048.
- Wimberger, P.H. 1984. The use of green plant material in bird nests to avoid ectoparasites. *Auk*, **101**: 615–618.