

Experimental demonstration of the energetic cost of parasitism in free-ranging hosts

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SUMMARY

Although some parasites have obvious pathogenic effects, others appear to have subtle, indirect effects that are poorly understood, particularly in natural populations. Indirect effects may result from parasites altering host metabolic rate and hence host energy needs, yet no experimental studies have shown this to be the case for non-laboratory hosts. We report the results of a long-term field experiment designed to test the impact of parasites on host energetics. We measured the energetics of feral rock doves (*Columba livia*) with populations of feather-feeding lice, traditionally considered to have little or no effect on host fitness. The lice reduced feather mass leading to increased thermal conductance and metabolic rate, as well as a steady reduction in host body mass over the course of the nine-month study. Our results demonstrate that even classically 'benign' parasites such as feather lice can reduce host condition through the accumulation of subtle energetic costs over time. We argue that experimental manipulations are a prerequisite for documenting such effects.

1. INTRODUCTION

How parasites affect host fitness is a central problem in host-parasite biology (Toft *et al.* 1991). Although some parasites have obvious negative effects on the host, others appear to have indirect effects. For example, laboratory studies of diverse taxa show that parasites are capable of altering host energy needs. Host metabolic rate is significantly reduced in polychaete worms (*Leonereis culveri*) with trematodes (Vernberg & Vernberg 1971), canaries (*Serinus canarius*) with malaria (Hayworth *et al.* 1987), laboratory mice with roundworms (Kilgore *et al.* 1988), and starlings (*Sturnus vulgaris*) with acanthocephalan worms (Connors & Nickol 1991). Metabolic rate is significantly increased in the case of sticklebacks (*Gasterosteus aculeatus*) with tapeworms (Lester 1971; Meakins & Walkey 1975). These studies demonstrate that parasites can affect host metabolism, yet the relevance of such effects to free-ranging populations of hosts is unclear.

Munger & Karasov (1989) detected no metabolic effects of tapeworms on wild mice (*Peromyscus leucopus*), despite a 2% drop in the digestive efficiency of infected mice in the laboratory. In contrast, Schall *et al.* (1982) presented correlational data showing a 15% reduction in the metabolic rates of lizards with natural malaria infections. Correlational studies are open to question, however, because of the possibility that a third variable, e.g. poor nutrition, drives the correlation of infection with lowered metabolism. As emphasized by

Keymer & Read (1991), testing the direct effect of parasites on host fitness calls for the experimental manipulation of parasite load.

Furthermore, because parasites generally show an aggregated distribution among host individuals (most have few parasites and a few have many (Anderson & Gordon 1982)), indirect effects are easily overlooked unless very large samples are studied. Manipulating parasite load, within the range of natural variation, can alleviate this problem by converting the aggregated distribution of parasites into a bimodal distribution of 'high' and 'low' load hosts.

We manipulated populations of feather-feeding lice (Phthiraptera: Ischnocera) on feral rock doves (*Columba livia*) to test the impact of parasites on the energetics of a free-ranging population. Ischnoceran lice, which occur on most bird taxa, are traditionally thought to have little or no effect on host fitness (Rothschild & Clay 1952; Ash 1960; Marshall 1981). Ischnocera feed only on dermal debris and feathers, and are not known to vector other parasites (Clayton 1990). However, it is possible that the feather damage they cause reduces plumage insulation, requiring an increase in thermoregulatory energy expenditure by the host. This is the hypothesis we set out to test.

2. METHODS

We manipulated louse loads by impairing host preening ability, the major defence of birds against ectoparasites (Marshall 1981; Clayton 1991). Preening was impaired with 'bits', small (< 0.8 g) C-shaped pieces of plated steel inserted between the mandibles of the bill and crimped slightly in the nostrils to prevent dislodging (but not enough to pierce the

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tissue). Bits create a 1.0–3.0 mm gap between the mandibles which prevents the full occlusion of the bill necessary for efficient preening.

To control for undetected side effects of bits (none were apparent), we bitted all birds in the experiment, then fumigated controls with a 1.0% pyrethrum solution that kills lice with no side effects on the host (growth trajectories of ten young squabs fumigated with pyrethrum did not differ significantly from those of ten unfumigated controls; $F = 0.22$, $p = 0.64$ (D. H. Clayton & D. Tompkins, unpublished results)). Unless fumigated, bitted birds experience a dramatic increase in louse load which mimics increases on birds with minor bill deformities (three of 150 birds censused for lice over a 3 week period (Clayton 1989)). Bit-induced variation in louse load does not, therefore, exceed the range of natural louse loads.

In May 1990 we captured 83 rock doves roosting under a bridge spanning Rock Creek on the border of Manteno, Illinois, U.S.A. (41° 15.0' N, 87° 50.3' W). All birds were banded, bitted, weighed and randomly assigned to 'low-load' or 'high-load' treatments. Low-load birds were fumigated, and high-load birds were sham-fumigated with water. All birds were then released at the capture site. Birds were recaptured and retreated in early July, late August and mid-October to prevent exponential increases in the louse loads of reinfested low-load birds (such increases tend to occur during the third month following reinfestation, but do not occur during winter in Illinois (D. H. Clayton, unpublished observations)). The birds were recaptured for a final time in February 1991, 9 months after the start of the experiment.

Louse loads were estimated as a categorical variable on two occasions (July 1990 and August 1990) and as a continuous variable at the end of the study (February 1991). The treatment status of birds was unknown during all estimation procedures. For the categorical procedure, chosen to minimize handling time in the field, the number of lice on the undersurface of one wing was scored visually as: 1, low; 2, moderate; 3, high; 4, very high. The number of lice on the rump (AR + PR; figure 1) was scored in the same way. The wing and rump scores were then added to provide an overall score for each bird in the range 1–8. The continuous procedure for estimating louse load at the end of the study, described in Clayton (1991), relies on regression models for estimating loads from timed counts of lice on several body regions ($r^2 \geq 0.82$).

Of 70 birds recaptured in October, random samples of 12 individuals from each treatment were held captive and transported to the laboratory for respirometry measurements. The birds were housed individually in 45 cm × 35 cm × 35 cm wire cages (one per cage) for up to 2 weeks before being released at the bridge. The cages were located on a roofed veranda with three sides open to the environment. All cages were separated by several inches to ensure against movement of lice (*Ichnocera* are physically incapable of leaving the body of the host except through direct contact between hosts (Clayton 1991)). Birds were provided with corn and drinking water ad libitum, but were deprived of food during the 28 h before the lab work.

Respirometry sessions were done at night to obtain measurements from birds in the resting phase of their circadian rhythm. Two birds, one low-load and one high-load, were measured simultaneously during each session: 1 h before natural darkness, each bird was weighed to the nearest gram on an electronic balance. A 36 gauge thermocouple was then inserted approximately 2 cm into the cloaca and secured with cyanoacrylate glue. Thermocouples were dislodged from 15 of the birds during the course of 48 trials.

Each bird was placed on a wire mesh platform in a small plexiglass respiratory chamber (10 cm diameter × 25 cm long). A thermocouple was positioned 4 cm from the gas exit port of each chamber. Both chamber and body temperature thermocouples were calibrated to 0.1 °C against an NBS traceable thermometer. The two chambers were then placed in a darkened temperature cabinet to provide ambient temperature control (± 0.1 °C). Dry, carbon dioxide free outside air was pumped through flowmeters into the chambers at 2–2.5 L min⁻¹ (which prevented oxygen concentration in the chamber from decreasing below ambient concentration by more than 0.5%). A sample of the gas exiting each chamber was directed through Drierite and Ascarite to remove water vapour and carbon dioxide before entering a dual-channel oxygen analyser (Applied electrochemistry S3-A). The oxygen analyser had dry, carbon dioxide free outside air pumped through its reference channel.

After a 50–60 min initial acclimation period at 22–25 °C, a 10–20 min record of oxygen consumption (\dot{V}_{O_2}) was made for each bird to determine basal metabolic rate; \dot{V}_{O_2} was calculated by using equation 4a of Withers (1977). Body temperature (T_b) was also noted. Ambient temperature (T_a) was then decreased by 5–10 °C and \dot{V}_{O_2} was again measured after 40–60 min. Chamber temperature was repeatedly lowered and \dot{V}_{O_2} measured until an ambient temperature of –10 °C was reached. Standard \dot{V}_{O_2} at each temperature was taken as the lowest consistent 2 min value within a 10–20 min period of continuous recording.

Thermal conductance (tc) was calculated by first converting \dot{V}_{O_2} into heat production by using an oxygen-calorific value of 18.8 J ml⁻¹ O₂ (assuming a respiratory quotient of 0.8 (Schmidt-Nielsen 1987)) and dividing this number by the difference between T_b and T_a . These calculations give 'wet' tc because it fails to take into account the heat lost from the body by evaporation. However, at temperatures below 20 °C, heat lost by evaporation in rock doves is relatively constant and small (< 10% of metabolic heat production (Calder & Schmidt-Nielsen 1967)), so the difference between 'wet' and 'dry' tc is small. In cases where T_b was not available because of a dislodged thermocouple, tc was calculated on the basis of the average T_b of birds of the same treatment measured at similar ambient temperature. Minimal thermal conductance for each bird was determined by averaging tc values at temperatures below the thermal neutral zone (< 20 °C).

In February only 24 birds were recaptured, and all of these were used for repeat respirometry measurements. Of the birds measured in October, 11 (5 low-load, 6 high-load) were remeasured in February. Recapture rates in both months were independent of experimental treatment (October, $G = 0.04$, $p = 0.85$; February, $G = 0.20$, $p = 0.66$). The small number of birds recaptured in February reflected a drop in population at the roost, presumably owing to a flash flood which submerged the bridge in November.

3. RESULTS

The combination of biting and fumigation resulted in high-load birds having significantly larger louse loads than low-load birds. The median louse score for 35 high-load birds examined in July was 4 (range, 2–5) compared with a median score of 2 (range, 2–4) for 31 low-load birds (Mann-Whitney, $U = 65$, $P < 0.0001$). The median score for 34 high-load birds examined in August was 5 (range, 4–6) compared with a median score of 3 (range, 2–5) for 32 low-load birds ($U = 225$,

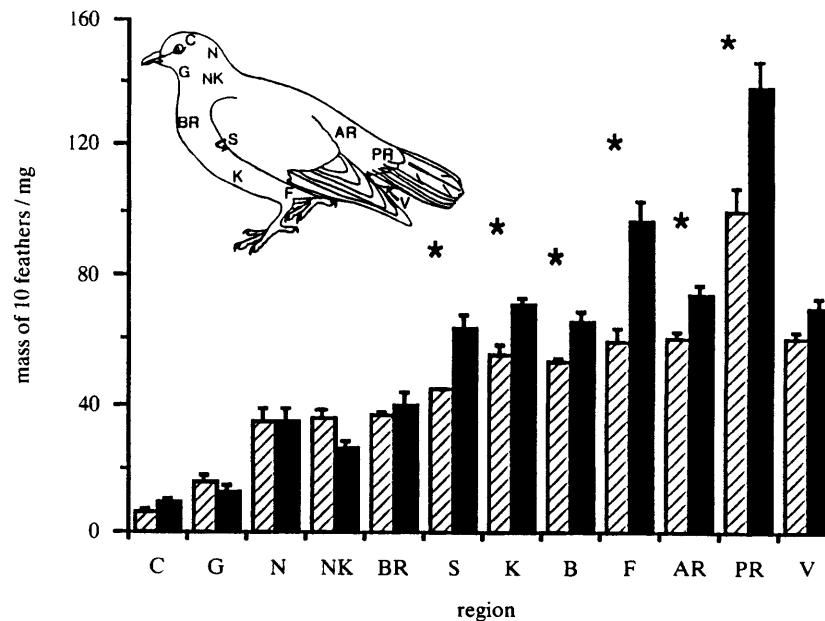


Figure 1. Mean (\pm s.e.) mass of feathers from 11 high-load birds (striped bars) and 13 low-load birds (solid bars) in February 1991. The value entered for each bird was the combined mass of the ten longest feathers of a clump plucked from each depicted body region: C = crown, G = gulum, N = nape, NK = side of neck, BR = breast, S = side (under wing), K = adjacent to keel, B = back, F = flank, AR = anterior rump, PR = posterior rump, V = ventral caudal tract. Wing and tail feathers were not sampled because they are not consumed by rock dove lice (Nelson & Murray 1971). The overall feather mass of high-load birds was significantly less than that of low-load birds (ANOVA $p = 0.005$); asterisks indicate regions contributing to the treatment effect (Fisher PLSD test, 0.05 level of significance).

Table 1. Mean (\pm s.e.) physiological parameters of feral rock doves parasitized by feather-feeding lice

(Body temperature (T_b) was measured by cloacal thermocouple and averaged across the five ambient temperatures shown in figure 2. The number of birds measured at all five temperatures (shown in brackets) is a subset of the total number because thermocouples were dislodged during the course of some trials. Basal metabolic rate (BMR) and minimal whole body thermal conductance (τ_c) were determined as described in the text.)

	low-load birds	high-load birds	significance ^a
October 1990 (<i>n</i>)	12	12	
body mass/g	336 \pm 8	324 \pm 7	$p = 0.215$
T_b /°C	38.9 \pm 0.2 [9]	39.2 \pm 0.1 [10]	$p = 0.080$
BMR/(mlO ₂ g ⁻¹ h ⁻¹)	0.833 \pm 0.016	0.904 \pm 0.028	$p = 0.019$
τ_c /mW g ⁻¹ °C ⁻¹)	0.231 \pm 0.004	0.259 \pm 0.010	$p = 0.016$
February 1991 (<i>n</i>)	13	11	
body mass/g	339 \pm 7	316 \pm 5	$p = 0.020$
T_b /°C	38.8 \pm 0.1 [9]	38.8 \pm 0.2 [7]	$p = 0.932$
BMR/(mlO ₂ g ⁻¹ h ⁻¹)	0.864 \pm 0.020	0.937 \pm 0.017	$p = 0.012$
τ_c /(mW g ⁻¹ °C ⁻¹)	0.205 \pm 0.004	0.222 \pm 0.005	$p = 0.014$

^a Student's *t*-test, two-tailed.

$p < 0.0001$). The mean louse load of the 11 high-load birds recaptured the following February was 450 lice (s.d. = 247) compared with a mean load of 104 lice (s.d. = 60) for 12 low-load birds ($T = 4.7$, $p < 0.0001$). In short, high-load birds were host to significantly more lice than low-load birds throughout the study.

High-load birds suffered more feather damage than low-load birds, as shown by a significant reduction in feather mass (figure 1). The reduction in feather mass was associated with an increase in whole-body thermal conductance (table 1), suggesting that feather damage decreased the insulative effectiveness of the plumage.

Increased thermal conductance should lead to a

reduction in body temperature unless compensated for by an increase in metabolism (Schmidt-Nielsen 1987). The body temperature of high-load birds did not differ significantly from that of low-load birds. In contrast, the metabolic rate of high-load birds averaged 8.5% higher than that of low-load birds. These results suggest that high-load birds maintained a constant body temperature, despite increased thermal conductance, by elevating their metabolic rates. The elevated rate persisted across a range of ambient temperatures in both October and February (fig. 2), suggesting that it was sustained through the autumn and into winter.

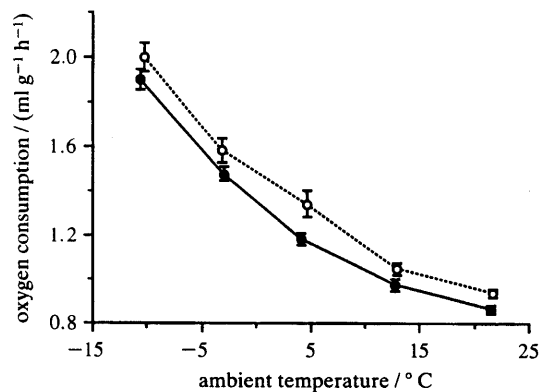


Figure 2. Mean (\pm s.e.) oxygen consumption (metabolic rate) at different ambient temperatures for 11 high-load birds (open circles) and 13 low-load birds (filled circles) in February 1991. The oxygen consumption of the former was significantly greater than that of the latter ($p < 0.001$, ANCOVA). Similar results were obtained from birds in October 1990.

4. DISCUSSION

The thermal conductance of high-load birds was greater than that of low-load birds, yet both groups maintained the same body temperature. These results show that high-load birds produced additional heat when cold stressed. The fact that the metabolic rate of high-load birds averaged 8.5% higher than that of low-load birds is consistent with the production of additional heat. This elevated level of heat production may have been mediated by an increase in circulating thyroid hormones, which are known to increase metabolic rate in endotherms (Eckert *et al.* 1988). Even during periods when the high-load birds were not cold stressed, metabolism was above normal, as reflected by an elevated basal metabolic rate (table 1). An increase in circulating hormone could be responsible for the fact that metabolic rate remained elevated during these periods.

Sustaining an elevated metabolic rate requires an increase in energy supply. Such an increase can be achieved by consuming more food, reducing activity, and tapping stored energy reserves. We did not attempt to quantify foraging or other activity in this study. However, even if high-load birds foraged more or were less active than low-load birds, these adjustments were apparently insufficient to balance the higher energy needs of the former. High-load birds lost body mass steadily over the course of the study relative to low-load birds (figure 3), suggesting that stored reserves were needed to maintain the elevated metabolic rates of the high-load birds.

Within species of birds, adult body mass is positively correlated with survival rate at cold temperatures (Stuebe & Ketterson 1982). The results of our experiment predict that the overwinter survival rate of high-load birds would be lower than that of the heavier, low-load birds. The long-term survival of most birds in our study could not be compared because > 70% of the population was lost (see Methods). However, an earlier field study of a nearby population using the same techniques demonstrated a significant

reduction in the overwinter survival of high-load rock doves (D. H. Clayton & D. Tompkins, unpublished results). The effect of lice on host energetics and body mass documented in the present study may well be responsible for this previously demonstrated effect of lice on host survival.

It is unlikely that lice had any effect on high-load birds other than causing an increase in thermoregulatory energy expenditure. Rock dove *Ischnocera* feed only on the basal barbules of abdominal contour feathers (Nelson & Murray 1971); thus, they probably have no effect on host flight ability. Furthermore, elevated loads do not cause irritation or an increase in preening rates (Clayton 1990), apparently because *Ischnocera* have appendages so highly specialized for locomotion on feathers that they do not go on the skin of the host (Marshall 1981; Stenram 1956). In other words, the louse-control function of preening in this system is apparently density independent (Clayton 1990).

The increased thermoregulatory energy demand caused by lice may affect components of host fitness other than survival. A previous study showed that male rock doves with high louse loads engage in less courtship display and obtain fewer mates than males with low loads (Clayton 1990). The low display rate of high-load birds may have been caused by the energetic consequences of lice. Courtship display is known to be energetically expensive (Ryan 1988; Vehrencamp *et al.* 1989).

Ischnocera lice are traditionally considered benign parasites (Ash 1960; Marshall 1981; Rothschild & Clay 1952). Our results strongly suggest that *Ischnocera* present a serious threat because their effect on plumage can lead to a reduction in host fitness mediated by the thermoregulatory cost of plumage damage. It is therefore critical for birds to invest regular time and energy in preening behaviour to keep populations of these lice in check.

Effects of parasites can be difficult to measure in natural populations because heavily parasitized individuals are generally uncommon (Anderson & Gordon 1982; Fowler & Williams 1985). This feature of host-parasite biology may explain why correlational studies often fail to detect costs of parasitism (Ash 1960; Hutson 1980; Bennett *et al.* 1988). Had we not boosted the number of heavily parasitized birds in our study, we probably would have failed to detect the energetic cost of lice. Thus we suggest that it is premature to conclude from correlational data alone that parasites have no effect on the fitness of wild hosts. Experimental manipulations of parasite load, within the range of natural variation, are required to test for potential effects of parasites, especially indirect effects such as energetic costs. To our knowledge, this study represents the first experimental demonstration of such costs in a free-ranging host population.

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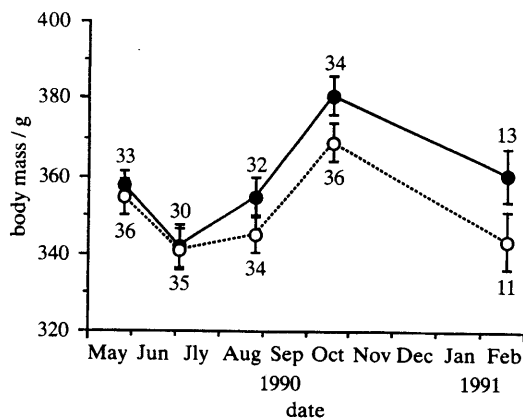


Figure 3. Mean (\pm s.e.) body mass of high-load birds (open circles) and low-load birds (filled circles) in the field over the course of the study. Numbers above and below the error bars indicate sample sizes. Empirical Bayes estimates (Sternio *et al.* 1983) and a cubic polynomial model were used to analyse variation in body mass. The linear component was significantly different between treatments ($p = 0.015$), indicating that high-load birds lost mass compared with low-load birds as the study progressed.

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