OIKOS 97: 223–228, 2002

Low humidity reduces ectoparasite pressure: implications for host life history evolution

Brett R. Moyer, Devin M. Drown and Dale H. Clayton

Moyer, B. R., Drown, D. M. and Clayton, D. H. 2002. Low humidity reduces ectoparasite pressure: implications for host life history evolution. – Oikos 97: 223–228.

A parasite's potential effect, or "pressure", can influence the life history strategy of its host. In environments with high parasite pressure, hosts invest more in anti-parasite defense, which may limit their investment in other life history components, such as survival. This tradeoff is difficult to study in natural populations because pressure is hard to quantify. Pressure is not necessarily correlated with the abundance of the parasite. A host population can be under high pressure, yet have few parasites, because members of the population have invested heavily in defense. Therefore, the extent to which parasite pressure varies among host populations, and the cause of such variation, remain largely undocumented. In this paper we show that birds in arid regions have fewer ectoparasitic lice than birds in humid regions. We show experimentally that low humidity reduces the number of lice on birds, even when host defense is held constant. Comparisons of ambient humidity to humidity beneath the plumage demonstrate that plumage does not provide a buffer for lice against low humidity. Our results confirm that an abiotic factor can cause substantial variation in parasite pressure among host populations. We suggest that humidity may influence host life history evolution through its impact on ectoparasites.

B. R. Moyer, D. M. Drown and D. H. Clayton, Dept of Biology, Univ. of Utah, 257 S. 1400 E., Salt Lake City, UT 84112, USA (clayton@biology.utah.edu).

Parasites have a fundamental influence on the ecology and evolution of their hosts (Loye and Zuk 1991, Toft et al. 1991, Crawley 1992, Grenfell and Dobson 1995, Clayton and Moore 1997). Maintaining defenses against parasites can be costly for hosts, forcing them to allocate limited resources to defense rather than other life history components (Sheldon and Verhulst 1996, Norris and Evans 2000). Recent studies have documented tradeoffs between investment in anti-parasite defense and components of host fitness, including survival (Moret and Schmid-Hempel 2000), reproductive success (Ilmonen et al. 2000), and competitive ability (Kraaijeveld and Godfray 1997). A host's investment in defense depends on the parasite's potential effect, or "pressure", on that host. However, the extent to which parasite pressure varies among host populations remains largely undocumented because pressure is difficult to quantify.

The abundance of parasites in a host population is not a reliable index of parasite pressure because host defense can also have a strong influence on abundance (Schmid-Hempel and Koella 1994). One way to clarify the influence of parasites is to decouple pressure from defense by experimentally suppressing defense. Immune defenses are difficult to suppress without influencing other important aspects of host physiology (Norris and Evans 2000). In some host-parasite systems, however, defense is not immunological, but involves other mechanisms that are much easier to manipulate, such as anti-parasite behavior (Hart 1997). We used such a system to explore how and why parasite pressure varies among host populations.

We studied birds and feather-feeding lice (Insecta: Ischnocera), which pass their entire life cycle on the body of the host (Marshall 1981). When present in

Accepted 5 December 2001

ISSN 0030-1299

large numbers, feather lice have a direct impact on host fitness. The feather damage they cause leads to energetic stress, with a resulting decrease in body mass and overwinter survival (Clayton et al. 1999). Large numbers of lice also reduce the attractiveness of birds to potential mates (Clayton 1990). Birds control feather lice primarily by preening (Hart 1997), a defense that is easy to manipulate (see below).

First, we compare the abundance of lice among populations of birds in different geographic regions. Our results show that birds in arid regions have many fewer lice than conspecifics in humid regions. We then show experimentally that low humidity causes reductions in the abundance of lice on birds, even when host defense is held constant. Comparisons of ambient humidity to humidity beneath the plumage demonstrate that plumage does not provide a buffer for lice against low humidity. Our results indicate that ambient humidity can have a dramatic effect on ectoparasite pressure. This effect may have important consequences for host life history evolution.

Materials and methods

Geographic comparisons of louse abundance

We compared the abundance of lice on live-trapped mourning doves (*Zenaida macroura*) and inca doves (*Columbina inca*) in two geographic regions, one arid and the other humid. The two regions were Tucson, Arizona (average monthly afternoon relative humidity = 25%, range = 13–34%) and Weslaco, Texas (mean = 60%, range = 55–67%) (National Climatic Data Center). Birds were captured using mist nets at the University of Arizona College of Agriculture Dairy Farm in Tucson, Arizona (Spring-Summer 1998), and at the Adams Unit of the Las Palomas State Wildlife Refuge in Weslaco, Texas (Spring-Summer 1998–99). We quantified lice using a fumigation chamber charged with ethyl acetate (Clayton and Drown 2001). Each bird was suspended in the chamber for 20 minutes with an adjustable draw string collar. Following fumigation and release of the bird, we overturned the chamber on a clean white sheet of paper, which was searched carefully with a 2× magnifying headset. We examined the chamber for additional lice, then wiped it clean. Lice were preserved in 95% EtOH, and later mounted on microslides and identified.

We also compared the abundance of lice on live-trapped rock doves (*Columba livia*), or "feral pigeons", in two geographic regions, one relatively arid and the other more humid. The two regions were Salt Lake City, Utah (average monthly afternoon relative humidity = 43%, range = 22–71%) and Manteno, Illinois (mean = 63%, range = 54–71%) (National Climatic Data Center). Birds were captured using walk-in traps in Salt Lake City, UT (Spring 1997) and in Manteno, IL (Spring 1988). We quantified lice using regression models that predict total abundance ($r^2 \geq 0.73$; $P < 0.0001$) from timed visual counts of lice observed on various body regions (Clayton and Drown 2001).

Impact of ambient humidity on louse abundance

To test the direct impact of humidity on louse abundance, we randomly assigned 48 infested feral pigeons to four humidity treatments. Pigeons were housed individually in wire mesh cages and provided with grain (Wheatland Seed Inc., Pigeon Mix), grit, and water ad libitum. Humidification lines were used to create mean ambient relative humidities of 17%, 38%, 59%, and 85%. All birds were kept at a relatively constant temperature of 27°C.

To block host defense, we impaired the preening of all 48 birds using "bits", which are C-shaped pieces of plastic developed by the poultry industry. Bits are inserted between the upper and lower mandibles and are crimped slightly in the nostrils to prevent dislodging, but without damaging any tissue. Bits create a 1–3 mm gap between the mandibles that impairs the forceps action of the bill required for efficient preening. Bitting does not interfere with feeding and has no measurable side effects; it has been used successfully in several previous experiments with pigeons and lice (Clayton 1990, 1991, Booth et al. 1993, Clayton and Tompkins 1995, Clayton et al. 1999).

We quantified lice using timed visual counts (see above) of birds once a week for six weeks.

Impact of ambient humidity on plumage humidity

To determine how ambient humidity influences humidity beneath the plumage, the microhabitat for lice, we used a microsensor (15041 Humidity Transmitter, Vaisala Inc., Woburn, MA) to measure the relative humidity between the feathers and skin of captive pigeons. We glued a Velcro strip to the small (6 × 18 × 3 mm) sensor, and then attached it to an opposing Velcro strip, which was glued to the bird's rump with Neoprene adhesive (beneath the feathers). Plumage humidity was measured ten minutes following attachment of the sensor to the bird. Ambient humidity was measured by removing the bird and suspending the sensor in the empty cage. This procedure was repeated with four birds, each of which was measured sequentially at the four ambient humidities used in the previous experiment.

Table 1. Prevalence and abundance (intensity) of lice at arid versus humid sites. See text for statistical tests.

Host species	Arid sites				Humid sites			
	Location	Prevalence*	Intensity†	*n*	Location	Prevalence*	Intensity†	*n*
Mourning dove	Arizona	3	2.3 ± 0.8	296	Texas	79	10.7 ± 2.0	33
Inca dove	Arizona	0	–‡	50	Texas	79	12.5 ± 3.1	29
Feral pigeon	Utah	47	124.9 ± 14.2	62	Illinois	100	631.0 ± 38.4	147

* Prevalence = percent of hosts infested.
† Intensity is the mean number ($\pm$1SE) of parasites divided by the number of infested hosts.
‡ Intensity is undefined for an uninfested host population, as the denominator would be zero.

Results

Geographic comparisons of louse abundance

The prevalence of lice was much lower in Arizona than Texas for both mourning doves and inca doves (Table 1; Fisher's exact test for both species, $P < 0.0001$). The abundance of lice was also lower in Arizona than Texas for both species; infested mourning doves in Arizona had significantly fewer lice than those in Texas (Table 1; Mann-Whitney test, $Z = 2.9$, $P < 0.005$). The difference was even more striking in the case of inca doves, none of which had any lice in Arizona (Table 1).

Both the prevalence and abundance of lice on feral pigeons were significantly lower in Utah than Illinois (Table 1; prevalence, Fisher's exact test, $P < 0.0001$; abundance (intensity), Mann-Whitney test, $Z = 8.0$, $P < 0.0001$).

Impact of ambient humidity on louse abundance

At the start of the experiment all birds had lice, with a mean ($\pm$1 SE) of 491 ($\pm$46) lice per bird. The abundance of lice on birds in the four humidity treatments did not differ significantly (ANOVA on log transformed loads, $F_{3,44} = 0.16$, $P > 0.05$) at the start of the experiment.

By the end of the six week experiment only 3 of the 12 birds in the lowest humidity treatment had lice, whereas all 36 birds in the three more humid treatments were infested (Fisher's exact test, $P < 0.0001$). Thus, low ambient humidity had a highly significant impact on louse prevalence. Ambient humidity also had a highly significant impact on louse abundance (Fig. 1; ANOVA on (log) change in louse abundance, $F_{3,44} = 38.2$, $P < 0.0001$). After six weeks, the abundance of lice on birds in the lowest humidity treatment had decreased significantly more than in the other treatments (Tukey HSD, $P < 0.05$).

Impact of ambient humidity on plumage humidity

Plumage did not buffer the microhabitat of lice against low ambient humidity (Fig. 2). Humidity beneath the plumage was highly correlated with ambient humidity ($r^2 = 0.97$, $n = 16$, $P < 0.0001$).

Discussion

Our results show that an abiotic factor, ambient humidity, can cause dramatic variation in parasite pressure. We document geographical variation in louse abundance that is correlated with ambient humidity. Furthermore, we demonstrate experimentally that low ambient humidity causes a sharp reduction in the abundance of lice, even when host defense is held constant. Below we discuss the implications of such variation in parasite pressure for host life history tradeoffs.

Our field data (Table 1) show for several species of birds that individuals in arid regions (Arizona, Utah) have many fewer feather lice than conspecifics in humid regions (Texas, Illinois). The afternoon humidity of our Arizona site, which is in the Sonoran Desert, and our Utah site, which is in the Great Basin Desert, averages less than 25% r.h. during the summer months, and can drop below 5% at times (National Climatic Data Cen-

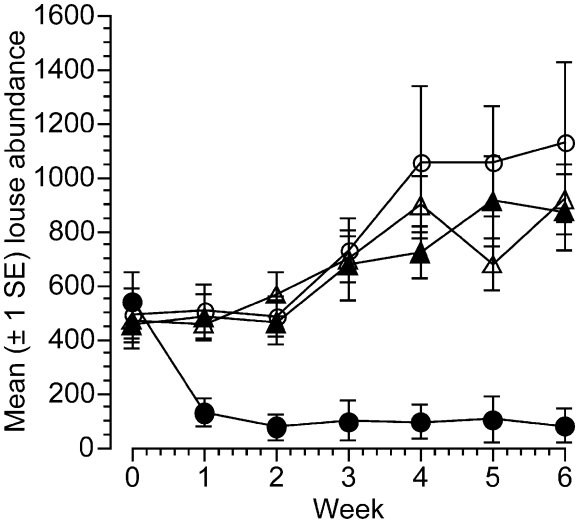

Fig. 1. Change over time in the abundance of lice on feral pigeons housed at 17% relative humidity (closed circles), 38% r.h. (open circles), 59% r.h. (open triangles), and 85% r.h. (closed triangles).

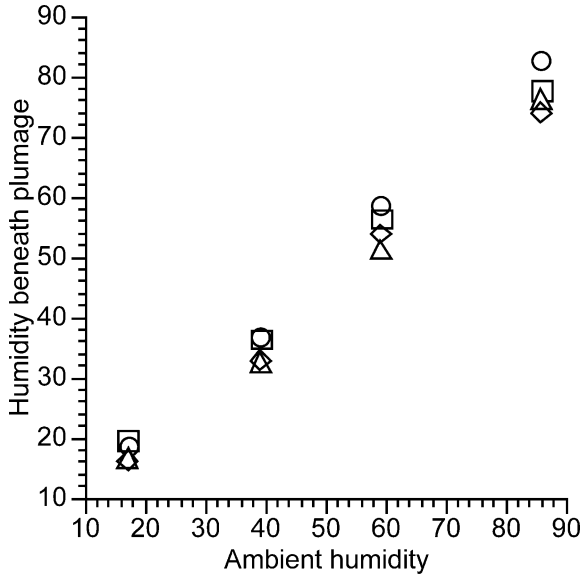

Fig. 2. Relationship of percent humidity beneath the plumage to percent ambient humidity. Each symbol represents an individual bird that was measured at four different ambient humidities (see text for details).

ter). By contrast, the afternoon humidity of our Texas and Illinois sites does not average less than 50% r.h. during any month (National Climatic Data Center). Although we found fewer lice on birds in the arid sites, there are clearly other factors, besides humidity, that differ between these sites. To clarify the impact of low humidity on louse abundance, we conducted a controlled experiment that manipulated ambient humidity, while holding all other factors constant. Low humidity characteristic of our arid sites caused a dramatic and rapid reduction in louse abundance (Fig. 1).

The proximal reason why lice do poorly at low humidity is probably that they cannot maintain sufficient water balance under such conditions. Many lice absorb moisture from the surrounding air using a water-vapor uptake system, but this method fails at low humidity (Williams 1970, Rudolph 1983). Rudolph (1983) used an ultrasensitive balance to monitor the weight change of individual lice at different humidities. He found that the water uptake rate of lice steadily decreases with decreasing relative humidity. Lice were unable to maintain their water balance below about 40% r.h. Our experiment shows that arid environments can desiccate plumage to a level far below this value (Fig. 2). Webster et al. (1985) used excised plumage patches from feral pigeons to measure how well plumage impedes the loss of water vapor. He concluded that the plumage does little to trap humid air near the skin surface, which is consistent with our results. Thus, although some earlier workers have assumed that feather lice are buffered from ambient conditions by their close association with the host's integument (Rothschild and Clay 1952, Marshall 1981), our results clearly show that plumage does not buffer lice against low ambient humidity.

Although the impact of low relative humidity on feather-feeding lice is clear, low humidity could conceivably have little effect on blood-feeding ectoparasites, given the high water content of their diet. On the other hand, many such parasites have more complicated life cycles than lice, including free-living stages that can be vulnerable to arid environments. For example, most fleas require relatively high humidity for proper development of the egg and (free-living) larval stages (Harwood and James 1979). This fact presumably explains why fleas are relatively scarce in arid regions (Amin 1966). Ambient humidity can also affect endoparasites, such as the free-living stage of nematodes that parasitize Scottish grouse (Hudson et al. 1985). Low humidity can cause larval desiccation, which reduces infection by this nematode (Prasad 1959). Humidity can also affect parasites through its influence on vectors. For example, a higher abundance of mosquitoes in wet Hawaiian forests appears to be responsible for the higher prevalence and abundance of avian malaria in wet forests, compared to dry forests (van Riper III et al. 1986).

The abundance of parasites in a host population is not a reliable index of parasite pressure because host defense can also have a strong influence on abundance. For instance, a host population can be under high pressure, yet have few parasites, because members of the population have invested heavily in defense. Thus, although studies have documented spatial variation in parasite abundance (Amin 1966, van Riper III et al. 1986, Bennett et al. 1992, Merilä et al. 1995, Figuerola 1999, Freeman-Gallant et al. 2001), they have not quantified variation in parasite pressure, independent of host defense.

An effective way to clarify the influence of parasites is to suppress host defense experimentally. Unfortunately, this approach is problematic for most parasites, because immune defenses are difficult to suppress without influencing other aspects of host physiology (Norris and Evans 2000). Feather-feeding lice are not impacted by the immune system (Clayton and Adams, in press). Preening, the principal defense against these lice, is easy to manipulate without side effects (see Materials and methods). The reduced abundance of lice at low humidity was therefore not the result of increased investment in defense by hosts. Rather, low humidity directly reduced louse abundance. Since Ischnoceran lice are known to reduce host fitness, our work provides a rigorous demonstration that parasite pressure varies due to an abiotic environmental factor.

Variation in parasite pressure can likely influence host life history strategies (Piersma 1997, Møller 1998). All organisms must allocate limited resources among competing life history demands, such as growth, repro-

duction, and survival (Stearns 1992). Host defenses against parasites can be quite costly (Kraaijeveld and Godfray 1997, Ilmonen et al. 2000, Moret and Schmid-Hempel 2000) and can constrain investment in other life history components (Sheldon and Verhulst 1996, Møller 1997, Norris and Evans 2000). Preening can be energetically expensive; e.g., Croll and McLaren (1993) documented a nearly 200% increase in the metabolic rate of preening thick-billed murres (*Uria lomvia*). This increase was higher than that associated with feeding (49%) or diving (140%). In addition to energetic costs, time spent preening cannot be devoted to other behaviors, such as foraging or courtship. Preening also reduces vigilance (Redpath 1988), possibly making birds more susceptible to predation. Given these costs of preening, we predict that birds in arid regions will spend less time preening than birds in humid regions. This simple hypothesis would be easy to test by measuring preening rates in the field (Clayton and Cotgreave 1994).

In summary, we document that spatial variation in the abundance of a parasite (feather-feeding lice) is correlated with a putative causal factor (ambient humidity). Unlike other studies, however, we also verify experimentally that this factor causes a reduction in the number of parasites on hosts, even when host defense is held constant. To our knowledge, this is the first study to demonstrate rigorously that parasite pressure varies substantially among host populations, and to verify the cause of the variation. Given the general sensitivity of parasites and their vectors to abiotic conditions, we suggest that abiotic factors may have an important influence on host life history evolution through their impact on parasites.

Acknowledgements – We thank S. Al-Tamimi, T. Jones, and S. Nelson for help with fieldwork. We also thank J. Allen, S. Benn, D. Blankenship, P. Else, B. Smith, M. Webster, and G. Waggerman for logistical assistance and advice. R. D. Price kindly assisted with louse identifications. We thank D. Penn, H. Richner, and S. Zala for helpful discussions and comments on the manuscript. This work was supported by an NSF CAREER award (DEB-9703003) to DHC, the University of Utah Research Awards Committee, and grants to BRM from Sigma Xi and the Frank M. Chapman Memorial Fund. The research presented here is described in Animal Research Protocols 96-09011 and 00-02002 approved by the Institutional Animal Care and Use Committee of the University of Utah. Fieldwork was done under permits to DHC from the U.S. Fish and Wildlife Service, Arizona Game and Fish Department, and Texas Parks and Wildlife.

References

Amin, O. M. 1966. The fleas (Siphonaptera) of Egypt: distribution and seasonal dynamics of fleas infesting dogs in the Nile Valley and Delta. – J. Med. Entomol. 3: 293–298.

Bennett, G. F., Montgomerie, R. and Seutin, G. 1992. Scarcity of haematozoa in birds breeding on the arctic tundra of North America. – Condor 94: 289–292.

Booth, D. T., Clayton, D. H. and Block, B. A. 1993. Experimental demonstration of the energetic cost of parasitism in free-ranging hosts. – Proc. Roy. Soc. Lond. B 253: 125–129.

Clayton, D. H. 1990. Mate choice in experimentally parasitized rock doves: Lousy males lose. – Amer. Zool. 30: 251–262.

Clayton, D. H. 1991. Coevolution of avian grooming and ectoparasite avoidance. – In: Loye, J. E. and Zuk, M. (eds), Bird-parasite interactions: ecology, evolution, and behaviour. Oxford Univ. Press, pp. 258–289.

Clayton, D. H. and Cotgreave, P. 1994. Relationship of bill morphology to grooming behaviour in birds. – Anim. Behav. 47: 195–201.

Clayton, D. H. and Tompkins, D. M. 1995. Comparative effects of mites and lice on the reproductive success of rock doves (*Columba livia*). – Parasitol. 110: 195–206.

Clayton, D. H. and Moore, J. (eds) 1997. Host-parasite evolution: general principles and avian models. – Oxford Univ. Press.

Clayton, D. H. and Drown, D. M. 2001. Critical evaluation of five methods for quantifying chewing lice (Insecta: Phthiraptera). – J. Parasitol. 87: 1291–1300.

Clayton D. H. and Adams R. J. In press. Chewing lice. – In: Thomas N. J., Forrester D. J., Hunter D. B. (eds), Infectious and parasitic diseases of wild birds. Iowa State Univ. Press.

Clayton, D. H., Lee, P. L. M., Tompkins, D. M. and Brodie, E. D. 1999. Reciprocal natural selection on host-parasite phenotypes. – Am. Nat. 154: 261–270.

Crawley, M. J. (ed.) 1992. Natural Enemies: The population biology of predators, parasites and diseases, 1st edn. – Blackwell Scientific Publications.

Croll, D. A. and McLaren, E. 1993. Diving metabolism and thermoregulation in common and thick-billed murres. – J. Comp. Physiol. B. 163: 160–166.

Figuerola, J. 1999. Effects of salinity on rates of infestation of waterbirds by haematozoa. – Ecography 22: 681–685.

Freeman-Gallant, C. R., O'Connor, K. D. and Breuer, M. E. 2001. Sexual selection and the geography of *Plasmodium* infection in Savannah sparrows (*Passerculus sandwichensis*). – Oecologia 127: 517–521.

Grenfell, B. T. and Dobson, A. P. (eds) 1995. Ecology of infectious diseases in natural populations. – Cambridge Univ. Press.

Hart, B. L. 1997. Behavioural defence. – In: Clayton, D. H. and Moore, J. (eds), Host-parasite evolution: general principles and avian models. Oxford Univ. Press, pp. 59–77.

Harwood, R. F. and James, M. T. 1979. Entomology in human and animal health. – Macmillan Pub. Co.

Hudson, P. J., Dobson, A. P. and Newborn, D. 1985. Cyclic and non-cyclic populations of red grouse: a role for parasitism? – In: Rollinson, D. and Anderson, R. M. (eds), Ecology and genetics of host-parasite interactions. Academic Press, pp. 77–89.

Ilmonen, R., Taarna, T. and Hasselquist, D. 2000. Experimentally activated immune defence in female pied flycatchers results in reduced breeding success. – Proc. R. Soc. Lond. B 267: 665–670.

Kraaijeveld, A. R. and Godfray, H. C. J. 1997. Trade-off between parasitoid resistance and larval competitive ability in *Drosophila melanogaster*. – Nature 389: 278–280.

Loye, J. E. and Zuk, M. (eds) 1991. Bird-parasite interactions. ecology, evolution and behaviour. – Oxford Univ. Press.

Marshall, A. G. 1981. The ecology of ectoparasitic insects. – Academic Press.

Merilä, J., Bjorklund, M. and Bennett, G. F. 1995. Geographic and indiviudal variation in haematozoan infections in the greenfinch, *Carduelis chloris*. – Can. J. Zool. 73: 1798–1804.

Møller, A. P. 1997. Parasitism and the evolution of host life history. – In: Clayton, D. H. and Moore, J. (eds), Host-parasite evolution: general principles and avian models. Oxford Univ. Press, pp. 105–127.

Møller, A. P. 1998. Evidence of larger impact of parasites on hosts in the tropics: investment in immune function within and outside the tropics. – Oikos 82: 265–270.
Moret, Y. and Schmid-Hempel, P. 2000. Survival for immunity: the price of immune system activation for bumblebee workers. – Science 290: 1166–1168.
Norris, K. and Evans, M. R. 2000. Ecological immunology: life history trade-offs and immune defense in birds. – Behav. Ecol. 11: 19–26.
Piersma, T. 1997. Do global patterns of habitat use and migration strategies co-evolve with relative investments in immunocompetence due to spatial variation in parasite pressure? – Oikos 80: 623–631.
Prasad, D. 1959. The effects of temperature and humidity on the free-living stages of *Trichostrongylus retortaeformis*. – Can. J. Zool. 37: 305–316.
Redpath, S. 1988. Vigilance levels in preening Dunlin *Caladris alpina*. – Ibis 130: 555–557.
Rothschild, M. and Clay, T. 1952. Fleas, flukes and cuckoos. – Collins, London.
Rudolph, D. 1983. The water-vapour uptake system of the Phthiraptera. – J. Insect Phys. 29: 15–25.
Schmid-Hempel, P. and Koella, J. C. 1994. Variability and its implications for host-parasite interactions. – Parasitol. Today 10: 98–102.
Sheldon, B. C. and Verhulst, S. 1996. Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. – Trends Ecol. Evol. 11: 317–321.
Stearns, S. C. 1992. The evolution of life histories. – Oxford Univ. Press, New York.
Toft, C. A., Aeschlimann, A. and Bolis, L. (eds) 1991. Parasite-host associations: coexistence or conflict. – Oxford Univ. Press.
van Riper III, C., van Riper, S. G., Goff, M. L. and Laird, M. 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. – Ecol. Monogr. 56: 327–344.
Webster, M. D., Campbell, G. S. and King, J. R. 1985. Cutaneous resistance to water-vapor diffusion in pigeons and the role of the plumage. – Physiol. Zool. 58: 58–70.
Williams, R. T. 1970. *In vitro* studies on the environmental biology of *Goniodes colchici* (Denny) (Mallophaga: Ischnocera). – Aust. J. Zool. 18: 391–398.