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ARTHROPODS—THE PELAGE OF MAMMALS AS AN ENVIRONMENT //

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INTRODUCTION

Most terrestrial and partially terrestrial mammals are covered with a hair coat within which are found a variety of arthropods, mostly ectoparasitic, which range from those that visit briefly to feed (blood-sucking flies and mites, argasid ticks) to those live within this habitat permanently (lice, mites). The adaptations to life in pelage are many, and the subtleties are best illustrated by examining the ecology of one group of permanent residents—the Phthiraptera—lice. /

The anatomical, physiological and behavioural adaptations of mammals for survival are numerous so there is a diversity of pelage habitats, which may be terrestrial or aquatic, small of large, or sparse or dense in hair. The whole life cycle of a louse is spent on the host so it is convenient to think of a louse population as that found on an individual host, isolated from others as if on an island. Upon their hosts the distribution and number of lice may be fairly static or change dramatically with season. However, as they are flightless, their island hosts must come in contact if lice are to disperse, survive and evolve. The opportunities to disperse from host to host depend upon the behaviour of the host. To survive lice must be able to breed and produce sufficient offspring to disperse to new hosts but the host of a louse is concurrently adapting to its environment, changing in physiology, behaviour, and population dynamics. The environment of a louse is not static so an adequate gene pool is required to survive change and exploit new niches.

THE HABITAT

The habitat in the pelage extends from the skin surface to the tip of the hair. An insulating blanket of stationary air is entrapped between the hair fibres so that a temperature gradient exists, the temperature range of which is usually determined by body and atmospheric temperatures. The slope of the gradient is influenced by the depth of the pelage and the density of hair.

A mechanism by which the host conserves heat is to restrict the flow of blood through the skin, particularly the extremities (feet, tail, ears, tip of nose, scrotum). This results in skin temperature dropping to approximately atmospheric temperature and in the virtual elimination of the temperature gradient. The temperature at the tip can rise when exposed to solar radiation, and temperatures as high as 70°C have been recorded in the fleece tip of sheep within 5 min of exposure to the sun. When this occurs the temperature gradient is reversed and temperatures near to the skin can rise to c 45°C.

Opening onto the skin surface are the orifices of the sweat and sebaceous glands. The proportion and abundance of these vary both over the body of a host and between host species. Their secretions determine whether a pelage is waterproof, the humidity of the microclimate, the ease with which a louse move through the pelage and the quality of its food. Humidity gradients exist within the pelage because there is a temperature gradient but, where a mammal does not sweat, the habitat can be arid.

Light varies in intensity with the time of day, and the depth to which it penetrates is influenced by the depth and density of the pelage.

At regular intervals a host sheds some of its pelage. This can be dramatic as in the elephant seal, which sheds annually the stratum corneum with hair attached, or the ox when it sheds its winter body coat in the spring. Less conspicuous are the hair-cycles that pass along the body of a mouse from nose to tail every few weeks, and inconspicuous is the shedding of the occasional hair from the mane or tail of a horse. Where the moult is seasonal, the result is a sudden change in the habitat of a louse as the reduced hair depth reduces the stability of the microclimate and increases the efficiency of grooming. The environment of a louse can change catastrophically.

BIOLOGY OF LICE

The life cycle of a louse comprises an egg, three nymphal instars and an adult male or female. All stages may be found together or eggs may be absent. Breeding areas are characterised by the presence of eggs, and their distribution is determined by the oviposition behaviour which is similar for the anopluran (blood-sucking) and ischnoceran (biting) lice of eutherian mammals. Eggs are attached singly to a hair near to the skin with the end of attachment nearest to the skin and the operculum distal.

There are three stages in the oviposition behaviour (Murray, 1957). Initially lice are attracted to warmth and select temperatures in the range usually found near to the skin, they then align themselves along the hair with the head towards the warm end of the gradient. Should temperatures be suitable, oviposition proceeds to the third stage when the louse turns around, thus reversing its alignment to temperature, and grasps a hair with a gonopod. The hair supplies a touch stimulus causing secretion of the cement substance followed by expulsion of the egg. The vertical distribution of eggs along the hair is determined by the depth of the temperature zone suitable for oviposition. The lateral distribution over the body is influenced principally by the type of hair and skin temperature. Where there is no hair, no eggs are laid unless a substitute is supplied artificially such as the clothing of man. If the hair is too wide to be held by the gonopod no eggs are laid, and thus the eggs of *Damalinia* spp. (biting-lice) are found only on the body whereas the eggs of the larger haematopinid lice (anopluran) are found also on the coarse hairs of the mane and tail. The eggs of lice are laid mostly at temperatures just below body temperature and no eggs are laid when thermoregulation reduces skin temperature to below 25°C. The eggs of *Haematopinus eurysternus* are more commonly found on the ears and tails of cattle in the summer than the winter for this reason.

Breeding areas are maintained when the eggs which have been laid and the resultant nymphs and adults survive the physical changes of the environment. There are two distinct stages in the development of eggs—morphogenesis and hatching, and the microclimatic requirements for each are not the same. Both require temperatures over 25°C, the optimal temperatures are usually between 32°C and 37°C, and the upper lethal temperatures are only a few degrees above body temperature (*c* 44°C). Temperatures below 25°C retard development but there is no evidence of suspended development. Morphogenesis proceeds over a wide range of humidities (8–100% RH) but RH's over 92% can be lethal at hatching (Murray, 1960).

Lice breathe through spiracles in the thorax and abdomen, and those on seals have a well developed apparatus to close the spiracle, probably to prevent entry of water into the trachea when the seal dives (Kim, 1971). Other modifications to the spiracles may play a role in water conservation.

Water conservation is a problem in a habitat where the temperatures for much of the activity is 33–38°C and humidities can be low. It is probably less of a problem for the blood-sucking Anoplura but is real for the ischnoceran lice, which absorb water from the atmosphere but are only able to do so when the RH is greater than 52% (Rudolph, 1983).

Should the physical attributes of the habitat favour the maintenance of breeding areas, a louse population can become established if the lice can feed, reproduce and disperse. Little is known of the details of the feeding behaviour. Anoplura suck blood directly from the venules (Lavoipierre, 1967), and the amount of blood taken and the frequency of feeding varies with species. Biting-lice (*Trichodectidae*) have mandibles and probably all, like *Damalinia* spp., feed at the skin surface. *D. ovis* of the sheep feeds on the keratinised outer layers of the stratum corneum and lipids of skin gland secretions (Sinclair, unpublished thesis, University of New South Wales, 1983). A considerable part of their diet is also the bacterial flora of the skin (Murray & Edwards, unpublished data).

The reactions of nymphal and adult lice to external stimuli depend upon their physiological state (e.g. oviposition behaviour). They have evolved to move along fibres, and many "wander" to the tip of the pelage where they may encounter lethal temperatures. More important are the short exposures to sublethal temperatures which reduce fecundity (Murray, 1963). Inadequate food also reduces the number of eggs laid. These factors in turn affect the reproductive potential of the species.

There are inherent differences in how lice disperse over the body. Some lay all their eggs within 3 cm², and their nymphs remain in this area until they disperse when adult. Others form nymphal and adult clusters while yet others disperse rapidly over the whole body. Those that move to the pelage-tip can disperse to a new host. They may be nymphs and adults or solely adult females, and the number transferred is related to the density of the population. It occurs principally when hosts touch one another, and mainly when mothers suckle young. The occurrence and duration of opportunities varies with host species.

Lice must produce sufficient offspring to assure survival. Their reproductive potentials vary greatly depending upon the number of eggs laid daily and generation time. These may be as many as 10 or as few as 0.4 daily and as long as 45 days or as short as 13 days, respectively. Some are parthenogenic, wholly or seasonally. It is here that lie major biological differences between lice (Fig. 1).

Morphological and biological differences between populations of *Pediculus humanus* on different parts

of the body of man (Busvine, 1948), and biochemical differences associated with the development of resistance to insecticides, as in *Linognathus africanus* (Baker, 1969) or *D. ovis* (Page, Brown & Flannagan, 1965), demonstrate that the genetic composition of a louse population can and does change, sometimes rapidly.
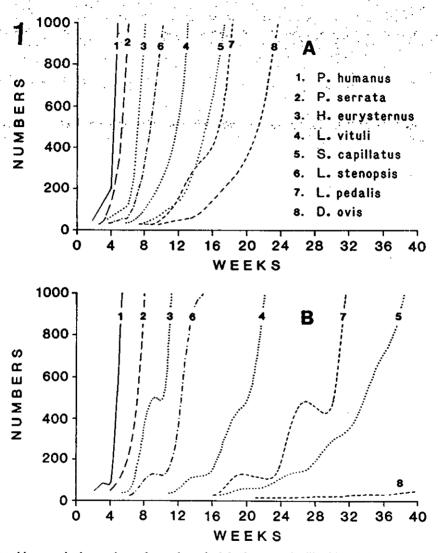

Fig. 1. Calculated increase in the numbers of nymphs and adults from one fertilised female louse for (A) zero mortality when females live 28 days, and (B) a mortality of 20% eggs and 30% nymphs when females live 14 days. The sex ratio is 1:1. The host, generation time and number of eggs laid daily are—*P. humanus* (man, 19, 10), *P. serrata* (mouse, 13, 2), *H. eurysternus* (ox, 28, 4), *L. vituli* (ox, 28, 1), *S. capillatus* (ox, 30, 0.6), *L. stenopsis* (goat, 29, 2), *L. pedalis* (sheep, 43, 1), *D. ovis* (sheep, 35, 0.4).

LOUSINESS

Lice on rodents have a restricted distribution on the body, usually to the head, upper neck, back and root of tail. On smaller rodents, mice, they may be virtually restricted to the head as the reduced surface area of a mouse enables grooming with the teeth to become extremely efficient (Murray, 1961). *Polyplax serrata* of the mouse has a high reproductive potential, achieved by reduction of the generation time (Fig.

1) because grooming has also selected for small lice with narrow abdomens in which only two eggs can develop daily.

Most small mammals shelter in burrows or nests, and are not exposed to extremes of climate. Large mammals are, and because of their size can carry a pelage of sufficient depth to insulate them from extreme cold. Heat loss is prevented from the slender extremities by restriction of the blood flow. The winter coat is shed in the spring and the summer coat is less thick. Cattle are fairly representative of large ungulates, and may be infested simultaneously with four species of lice whose distributions on the body differ. Numbers increase when the coat is long in the winter but fall rapidly when the winter coat is shed. The resultant decrease in the stability of the microclimate and increase in grooming efficiency are undoubtedly major factors causing the decline. The reproductive potentials of these lice, which are quite different (Fig. 1, see 3, 4 and 5), probably reflect the differences in the harshness of their environments during the summer. A feature of the habitat that can restrict availability of food for blood-sucking species is the immune reaction, which causes a local restriction of blood flow through vessels of the capillary network in the skin (Nelson, Bell, Clifford & Keirans, 1977). This phenomenon operates where lice become abundant as at end of a long winter, and probably where lice are confined to a part of the host's body as are *Linognathus pedalis* to the feet of sheep by a wool barrier. The dispersal of nymphs from a cluster of *H. eurysternus* on cattle after 2–3 weeks could be due to a local shortage of food caused by this immune reaction. The immune itch stimulates and directs grooming.

When hair-seals swim, the air between the hair of the pelage is replaced by water and the skin temperature drops to that of the sea. Lice are found on the hind flippers because here lice can feed rapidly when the skin temperature rises as the blood flow increases during heat dissipation. They survive between meals on seals at sea because the skin temperature is low, and in a state of suspended animation little nutriment and oxygen are required (Murray, 1976).

The reproductive potential of *P. humanus* of man is the greatest known (Fig. 1). Man, assisted by his technology, can groom very efficiently, and can shed his pelage (clothes) with unpredictable facility and rapidity, for a louse. But lice do survive, and erupt from foci with embarrassing frequency.

The marsupials of Australia also become lousy, and their boopiid lice belong to a third major sub-order, the Amblycera. Lice of this sub-order, like the Ischnocera, are found widely on birds and restrictedly on mammals. Their diets are more general; some feed on feathers, some on the surface of the skin, some on blood, and others are predatory on eggs and moulting nymphs (Nelson, 1971). They are biologically different from anopluran and ischnoceran lice. There is little reason at present to suspect that their pelage habitat on marsupials is much different from that on eutherian mammals but their survival in this environment appears to have been achieved by adaptations parallelling those of both anopluran and ischnoceran lice. They have failed to exploit this niche on six families of Australian marsupials (Murray & Calaby, 1971).

SUMMARY

The problem of lousiness in nature is usually not why are a few hosts heavily infested, it is why does the majority of the host population carry so few lice. The reproductive potentials described have probably been selected to enable these survivals. Anoplura have exploited the pelage of mammals the best. Their food, blood, is available over just about the whole body, and is a diet that supplies sufficient water for the increases in egg production only seen in this group. At least 70% of an egg is water. They have also a great capacity to change their generation time. The *Trichodectidae* feed at the epidermals surface on keratin, skin gland secretions and bacteria. These change in quality and abundance over the body and seasonally. The diet is limited in free moisture which together with the small size of the louse apparently restricts daily egg production. Parthenogenic reproduction is found in this group. Aspects of the biology of the *Boopiidae* on marsupials appear to parallel both anopluran and ischnoceran lice.

Several species may infest one host, and they or their strains may infest different parts of the same host. Their ecology is not the same, and what may be catastrophic to one is not necessarily catastrophic to another. Although it is convenient to consider a population of lice as that found on a single host, the evolutionary unit is a population of hosts. The environments within the pelages of a population of hosts are not identical, so some lice may survive catastrophies, the surviving populations providing the insects for subsequent dispersal and repopulation.

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