POPULATION REGULATION IN QUILL MITES (ACARINA: SYRINGOPHILIDAE)[1]

JOHN KETHLEY[2]
Acarology Laboratory, The Ohio State University, Columbus

Abstract. The wing quills of the House Sparrow (*Passer domesticus* L.) may host as many as three species of quill mites, suggesting ecological differences in the quill mite habitat. Detailed investigation of a single species of quill mite, *Syringophiloidus minor* (Berl.) reveals adaptations that maximize mite success within the confines of the feather calmus and suggests a mechanism that allows partitioning of the wing by two or more different-sized quill mite species.

Quill mites live inside the feather calmus and feed on host tissue fluids by piercing the quill wall with long styletlike chelicerae. Mite reproduction and development take place within the calmus. Only adult female mites disperse. Females can move into newly developing quills during host moult in the fall, or into the developing feathers of nestlings in the spring. The quills in which the mites live represent a closed system, with calmus volume limiting the number of mites that may mature and calmus wall thickness limiting the ability of the mites to feed. Female mites cease egg production before the quill contains enough mites to fill it. As a result, the quill does not become filled with immature forms that would be incapable of mating and dispersing. Males of *S. minor* are smaller than the females and have a frequency of exactly 1:11. Thus over 95% of the limiting resource, calmus volume, is occupied by females, the potential dispersants.

The size of a female is evidently limited by two opposing selective pressures: the smaller they are, the more can disperse from a given quill, but if they become too small the mouthparts will not be able to reach through the quill wall to feed. Thus each quill size has an optimum mite size, and the mite species occur in a corresponding diversity of sizes.

Quill mites live inside the shaft of the flight feathers and feed on tissue fluids by piercing the wall of the quill with their long, needlelike chelicerae. These mites are assigned to the family Syringophilidae which has long been regarded as a small, uniform group of nondescript bird parasites. Recently these mites have been shown to exhibit great diversity with most groupings of species limited to distinct sets of hosts, or parasitic habitats, or both (Kethley 1970). What was previously regarded as a group of a few species is now known to be a diverse family with a high degree of host specificity and because there are two, three, and even four species of quill mites on a single host species, the number of species will obviously be very great. It is not difficult to imagine diversity due to host specificity, but when a single bird has four species of quill mites, it is essential to search out some ecological explanation for diversity. To answer the general question of how there can be so many different species on one bird, it is necessary to start with studies of the population ecology of quill mites. A detailed account of the biology of one species of quill mite—*Syringophiloidus minor* (Berl.) (Fig. 1) from the House Sparrow, *Passer domesticus* L.—is used below to show how the mites exploit their resource and how the adaptations that limit quill mites to a portion of their possible habitats may have allowed the development of two or more mite species on a single host.

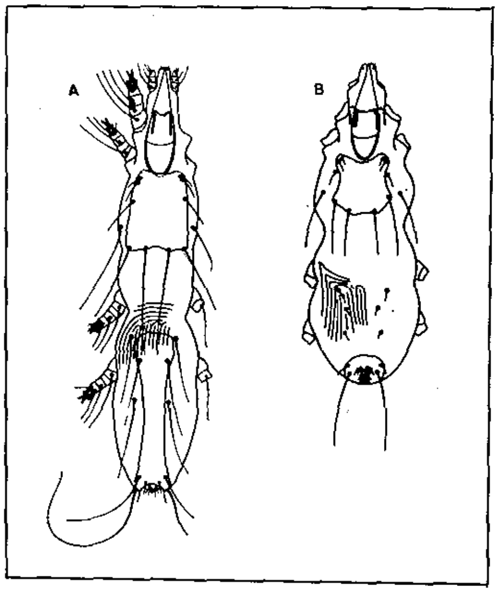

FIG. 1. *Syringophiloidus minor* (Berlese). Dorsal aspect: *A*, female; *B*, male. (100 X, male and female drawn to the same scale.)

METHODS AND MATERIALS

House Sparrows were trapped in Columbus, Ohio, with a Hav-a-hart sparrow trap from March 1969 to June 1970. Each quill of all flight feathers (pri-

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[2] Present address: Field Museum of Natural History, Division of Insects, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605.

maries, secondaries, tertiaries, greater primary coverts, greater secondary coverts, lesser and median coverts, and alular quills) was individually opened under alcohol and the contents of the calmus examined. When mites were present, the total number of individuals as well as the number of each age class were recorded for each occupied quill.

Observations of the Life Cycle of *Syringophiloidus minor* (Berl.)

In late summer, House Sparrows begin fall moult. At this time, one always finds at least one small, nulliparous (fertilized nongravid adult) female in every new quill that is occupied. The mites invade the open umbilicus of the developing feather. As the feather matures, the umbilicus closes and the mites can no longer enter. Only mature females are found in newly formed feathers, and in the majority of instances there is only a single individual present (Fig. 2). The younger feathers contain lightly colored small females, and these females are nonreproductive. Later the females become yellowish and the ovary enlarges and shows as an opaque white sphere in the translucent body. Such older females regularly contain one large egg. As the season progresses, eggs appear in the feather and these develop through the larval and two nymphal stages to the adult. The first adult to develop is a male, and the remaining 10–12 eggs develop into females. About the time the progeny of the first generation are maturing, the founding female ceases egg production and dies. The corpse of this female dries and is recoverable whenever the quill is opened in sampling. The young females, in turn, begin to produce 10–12 eggs, averaging one male and 9–11 females per female.

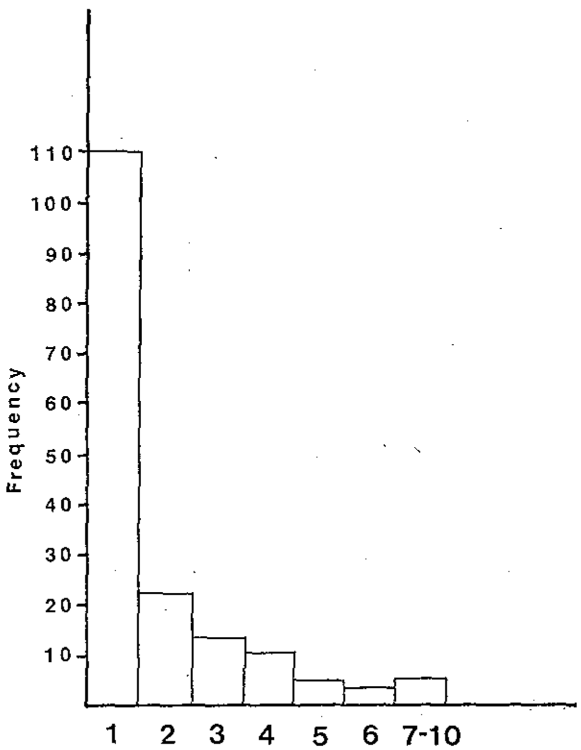

Fig. 2. Frequency of the number of founding females per quill for *Syringophiloidus minor* occurring on a sample of *Passer domesticus.*

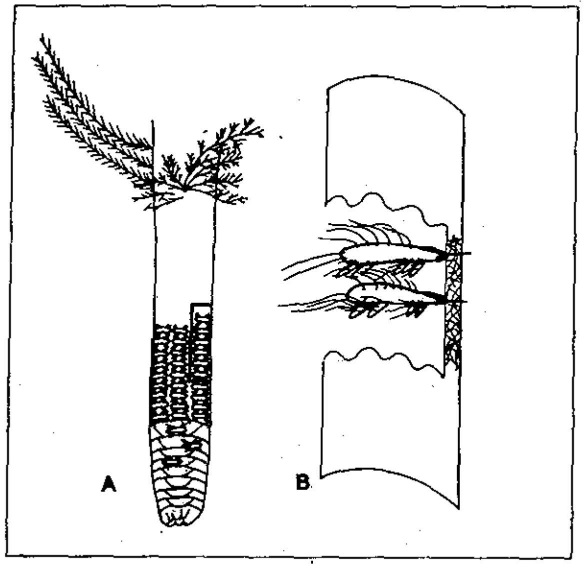

Fig. 3. Diagrammatic representation of *S. minor* inside quill: *A*, mites packed in lower half of the calmus; *B*, enlarged section of the quill showing mites feeding with their chelicerae inserted through the calmus wall.

The second generation matures by early spring. By then the volume of the mites in the tertiaries, secondaries, and some of the primaries equals 95%–100% of the volume of the calmus and the mites are so tightly packed in the feather that they can hardly move (Fig. 3). When these tightly packed quills are partially split for sampling at this time, they continue to open and the mites spill out into the study dish. The females in the packed feathers remain small and transparent and show no ovarian development. Populations in the larger primaries do not quite fill the quill and in these a few of the second-generation females are reproductive. The smaller quills are filled by 80–90 mites. Most of the secondaries and primaries contain 121 females and 11 males. It is clear that one female can produce enough mites in two generations to fill the feathers.

Quills with the corpses of two or three founding females also contain 120–130 young females. The first-generation counts indicate that with multiple founders each performs similarly to isolated females, but the total numbers in full quills were always around 120–130 young females. Obviously the females of the second generation produce fewer eggs. If there were no alteration of the reproductive rate, the feathers would be completely filled when the majority of mites were nymphs and further development would be impossible for lack of space. It seems clear that egg production is reduced as the feather tends to be filled with mites.

In the spring, the adult birds mate and rear their young. The transfer of mites has not been observed, but some of the mites must leave the adult hosts because the young birds leave the nest with some mites in their quills. Only adult female mites—usually one—are present in the newly formed feathers. The mite populations in the quills of young fledglings develop in the same way as those of adult hosts following the fall moult.

Some postnesting adult sparrows show a secondary infection in the primary coverts. The superior umbilicus of these feathers is permanently open. Between the fall moult and nesting, mites are found only in primaries, secondaries, and tertiaries, but postnesting hosts frequently harbored mites in the primary coverts in addition to the flight feathers. There is no evidence for movement of the mites among quills following completion of the fall moult and prior to host nesting, nor is there any evidence of dispersal between feathers after the nesting period. All occupied quills have a parallel development of the populations. The invasion of all quills of a host occurs over a short period of time and once a population is started in a quill there are no later invaders.

The successful dispersants in the coverts of adults begin to develop populations as described earlier, so that by the time fall moult begins, the quills are packed full with mites. Just before the old feathers are moulted, the young females leave and disperse to newly developing quills. The life cycle is summarized in diagrammatic form in Fig. 4.

Aspects of Population Regulation—Adaptations to the Resource

The nongravid female is the dispersal form, and during dispersal all young female mites compete for

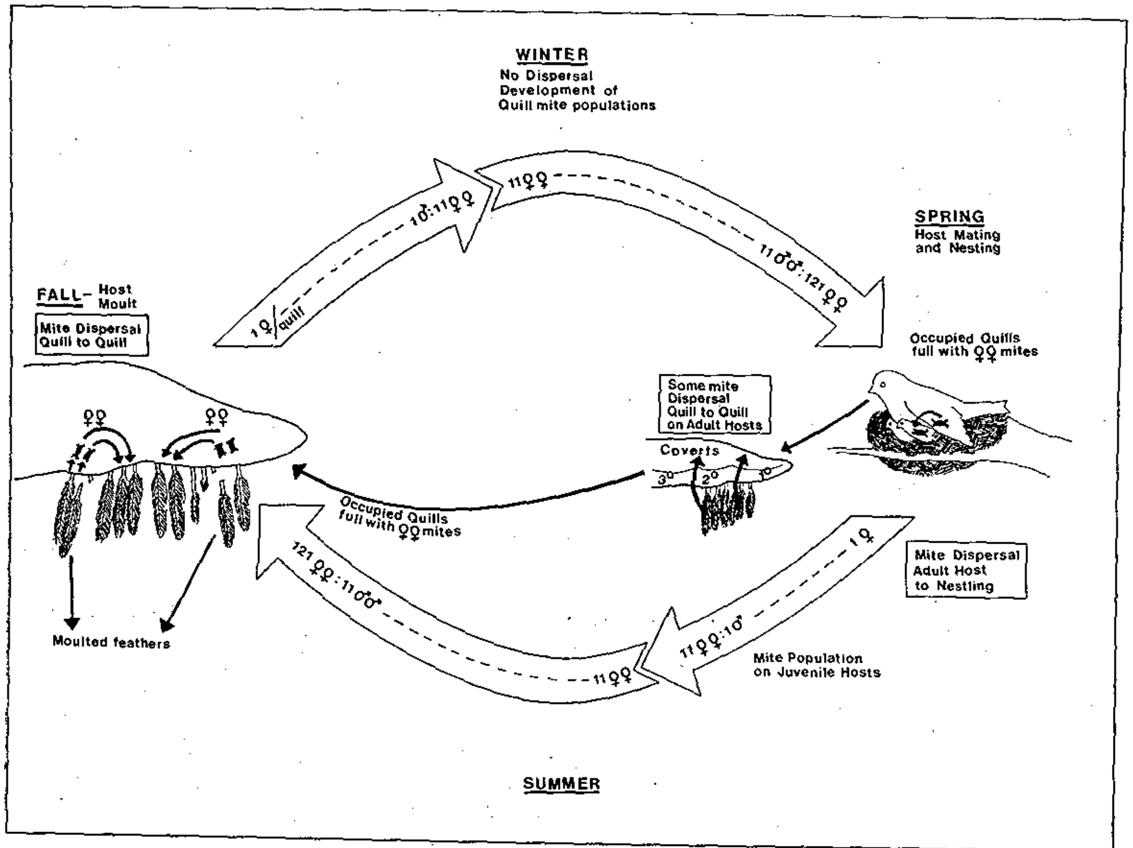

Fig. 4. Diagrammatic life cycle of the House Sparrow quill mite *Syringophiloidus minor*. Events of the host life cycle that are significant for the quill mite are given in their respective seasons (different positions on the diagram): host moult in the fall, mating and nesting in the spring. Rectangles indicate periods of mite dispersal: mite dispersal from old, about-to-be-moulted feathers to newly developing feathers on the same host individual in the fall; dispersal of mites from the adult host to young nestlings in the spring; dispersal of mites from the primaries and secondaries to the primary and secondary coverts of the adult hosts in the late spring. Broad arrows show development of mite populations per quill: one female produces one male and 11 females, each of which in turn produces one male and 11 females.

TABLE 1. Comparison of observed and expected number of founding females per quill

Number of founding females per quill	Observed	Expected[a]
1.	110	78.2
2.	22	54.1
3.	13	24.8
4.	10	8.6
5–10.	11	2.9
$\chi^2 = 38.56$, 4 df; $P << 0.01$		

[a]Calculated after Cohen (1960) for $\bar{x} = 1.846$, $N = 169$, $\lambda = 1.382$ where $P(x) = \frac{e^{-\lambda}(\lambda^x)}{x!\,(1-e^{\lambda})}$.

new feathers with other females. If dispersal among the flight feathers is at random, then a Poisson distribution would approximate the likelihood of site discovery and hence give an index of the expected number of females per quill. Since only quills occupied by mites are considered, the zero class is absent, and it is necessary to employ a truncated Poisson. Utilizing the method of Cohen 1960, it is possible to calculate a frequency of occurrence which can be compared with the observed values. As may be seen from Table 1, there is a significant departure from the observed values for the one, two, and three females per quill class. It is possible that the excess of single invasions reflects a regulatory mechanism that breaks down at extremely high densities.

A selective pressure for reducing the number of female invaders can be measured in terms of the mean number of daughters produced by various-sized founding groups. A single female in a quill can produce about 121 potential dispersants. Those females entering a quill with one other mite will each give rise to an average of 60 dispersants, and three founders will each average 40 progeny—totaling 120 mites. Obviously single females per quill contribute more than multiple founders so that a distinct advantage is gained by single founders, because they produce more potential dispersants.

A single female of *S. minor* and her progeny completely fill the space of the feather. Thus, feather volume fixes the maximum volume for the descendents of founding females. These descendents will colonize feathers, and females which produce more colonizers should have a selective advantage over females with less-numerous offspring. One way to obtain numerical advantage would be to disperse as immatures of small size, thus utilizing less space in the parent population.

This is not likely to be an advantageous tactic due to competition for space after founding. The first founder producing young will preempt space from other founders, thus the progeny of an adult invader would occupy the space of a feather more rapidly than the descendents of a larval or nymphal invader.

A second way of modifying the number of potential dispersants is to reduce the number of males. The House Sparrow quill mite has only one male per brood and thus can fill the remaining space with females. A further gain is achieved by keeping the male at a size just slightly larger than a full-grown larva. The gain over a population in which the sexes are equal in numbers and size is illustrated in Table 2. Of a total population volume of 124.5, 96.5% is devoted to potential dispersants, and only 3.5% is required for bisexual reproduction. The proportion of the population committed to dispersal, not only in numbers but also in biomass, is very high as compared with a 1:1 sex ratio.

The number of offspring per female is also limited by the calmus volume. In coverts, the maximum capacity for *S. minor* is 90–95 mites, whereas there are over 120 female mites in the primaries. There should be a selective advantage to colonize a large quill because these females can produce more daughters before exhausting the space resource. However, the larger feathers (primaries 7, 8, 9) were rarely occupied and those occupied contained either a dead female or a dead female with dead larvae. Evidently these mites fail because they cannot feed. These

TABLE 2. Effect of modification of sex ratio and male size on alteration of quill mite productivity for a hypothetical form having 12 progeny per female

Population structure	Relative volumes	Sex ratio	Number of dispersing females produced in two generations	Female volume/ Total mite volume
Sexes equal.	♂ = ♀	1:1	36	36/72 = 50%
Males less frequent.	♂ = ♀	1:11	121	121/132 = 91.6%
Males smaller and less frequent.	♂ = .4v♀	1:11	121	121/124.5 = 96.5%

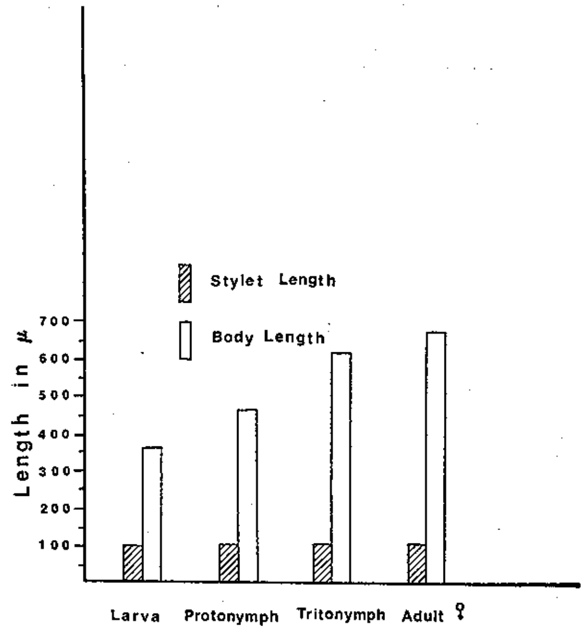

FIG. 5. Comparison of stylet length with body length for the life stages of *Syringophiloidus minor.*

feathers have the thickest walls, and if the stylets of the mites are too short to reach through the walls, then the population will fail. It would seem that the adult, a relatively large form, ought to be able to feed easily while the smaller larvae would be the stage to fail, if ability to pierce the wall were limiting. Yet there is evidence of high adult mortality in the large quills. This apparent inconsistency cannot be resolved by consideration of body size alone. When stylet length is examined, these mites show a remarkable similarity of stylet length in all developmental stages. The larvae have stylets equal in length to those of adults, and thus, the feeding limits are not related to body size (Fig. 5).

This suggests that larval size is as small as it can be and still allow the operation of stylets one-fourth of the body length. While larger size is an advantage in feeding, being too large is a disadvantage because fewer females can mature in a feather, thus, the yield of daughters can be maximized by keeping the female as small as possible. The female is only three times as long as the larva and can develop only one oocyte at a time. Consequently the population develops very slowly because of the long interval between depositing eggs. Selective pressures may favor females so small that they are able to nourish only a single egg at a time and this would set a lower limit to female size.

Size of a syringophilid may thus be fixed by two independent selection factors. The pressure to increase size and length of feeding organs tends to maximize size while the limited space of a feather results in an advantage to females that are small and are therefore able to maximize the number of descendents in a feather.

For a quill mite with a fixed volume, there is a range of quill volumes proportional to the mite volume which is optimal for that mite. Consequently, *S. minor* is limited to a certain range of feathers. In larger quills, *minor* fails because the mites cannot feed, and in smaller quills it fails because the mites cannot produce many dispersants. Those quills unsuitable to *minor* would be suitable to quill mites of a different size. A larger mite with longer stylets would be successful in those large quills in which *minor* starves. Likewise, a smaller form could produce more progeny and compete successfully in the smaller quills. The resulting differences in the sizes of the mites and concomitant restrictions to different quills might have allowed the development of genetically isolated forms. In looking at the known species of syringophilids one sees a range of mite sizes that represent an adaptation to a range of quill volumes. There are large mites in large quills and small mites in small quills, and if the large quills and small quills occur on the same host, then there are two sizes of quill mites on that host.

CONLUSIONS

The House Sparrrow quill mite, *Syringophiloidus minor,* lives inside the flight feathers and feeds on tissue fluids by piercing the wall of the quill with long, needlelike stylets. Reproduction and development take place within the confines of the quill. Nulliparous females enter at the superior umbilicus and found a colony in the newly developing quills of hosts during fall moult or in the newly developing feathers of nestlings. Once a population is established, there is no entrance or egress prior to host moult or nesting. Populations in quills have a parallel development. The life cycle of the mite is modified to maximize mite success within the confines of the feather calmus.

Two properties of the quills limit the mites: (i) the volume of mites that mature cannot excede the volume of the calmus and (ii) the calmus wall is a barrier which the mites can breach only if their stylets are (a) supple enough to work through the fibrous calmus wall and (b) long enough to reach the soft tissues surrounding the calmus.

The mite maximizes the number of female offspring per quill by ceasing egg production before the quill contains enough mites to fill the feather. The small male, with a frequency of 1:11, occupies less than 5% of the calmus volume, thus over 95% of the limiting resource, space, is occupied by females, the potential dispersants.

A quill mite will gain a selective advantage by reduced size because that will increase the number of dispersing females it can produce. At some point in size reduction the larvae will become so small that their stylets will be too short to pierce the calmus wall. At this point the selective gain from size reduction will be balanced by mortality due to failure to feed. If the opposing selective pressures are sufficiently strong, one would expect a characteristic-sized quill mite for each size of quill. This may account for both the diversity among different species of quill mite sizes, which range from 0.0014 mm^3 to 0.0866 mm^3 in volume, and the fact that when birds have two or more quill mites, the mite species differ greatly in size.

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