FAECES AVOIDANCE BEHAVIOUR IN UNISEXUAL AND BISEXUAL GECKOS

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The unisexual gecko, *Lepidodactylus lugubris*, harbours fewer types of parasites and has lower prevalence of infection than does the bisexual gecko, *Hemidactylus frenatus*, or its bisexual parental species. Because many diseases and parasites are transmitted through faeces, we conducted a series of experiments to examine whether or not *L. lugubris* had a greater tendency to avoid faecal matter than *H. frenatus*. The research found that both species defecated away from their daytime hiding places. The unisexual geckos, when given a choice, picked hiding places that were surrounded by clean rather than contaminated sphagnum moss, or places that were sprayed with distilled water rather than faecal solution. The bisexuals also displayed a tendency to pick hiding places surrounded by uncontaminated sphagnum moss, but, unlike the unisexuals, did not avoid faecal solution. Neither species avoided dried faecal matter. These data support our hypothesis that the unisexual gecko, *L. lugubris*, exhibits more parasite avoidance behaviours than the bisexual gecko, *H. frenatus*.

INTRODUCTION

The unisexual gecko, Lepidodactylus lugubris, harbours fewer types of parasites and has a lower rate of parasitism than the bisexual gecko, Hemidactylus frenatus, both in Hawaii (Brown et al., 1995) and throughout the Pacific Basin (Hanley, Volmer & Case, 1995). Lower parasitism rates are found for both endoparasites transmitted by the faecal-oral route and ectoparatsites, like mites. Hanley, Fisher & Case (1995) found that when L. lugubris lived in sympatry with either of its parental species, Lepidodactylus moestus and Lepidodactylus undescribed species (Radtkey et al., 1995), the bisexual parental species had a higher prevalence of - and more intense - mite infestations than the unisexual hybrid. Moreover, in their experiments on mite exposure, they found that in both mixed and single species conditions, more of the bisexual geckos contracted a mite infection than the unisexuals. Brown et al. (1995) obtained similar findings on mite transfer between L. lugubris and H. frenatus.

Continuing comparisons between disease rates and parasite avoidance behaviours in unisexual and bisexual species are important for testing the Red Queen hypothesis of the evolution of sex. The Red Queen hypothesis states that in the long term, bisexual species have an advantage over unisexual species in adapting to new parasites or to old parasites with newly evolved means of transmission or virulence (Seger & Hamilton, 1988). In the short term, however, unisexual species may have reduced prevalence of parasites compared to the bisexual species with which it lives in sympatry (Brown *et al.*, 1995).

Host species should evolve not only efficient immunological systems against disease organisms but also behaviours that enable individuals to avoid becoming parasitized. For example, Atkinson & Van Riper III (1991) hypothesized that Hawaiian forest birds now sleep with tucked up bills and faces and a raised leg to protect exposed skin from mosquito bites. These behaviours were not observed in endemic Hawaiian birds prior to the introduction of mosquitos that carried avian malaria and pox to the Hawaiian islands. Some species, such as chimpanzees, seek out and consume plants with compounds that kill off their parasites (Rodriguez & Wrangham, 1993), and recently Hemmes *et al.* (1995) reported that wood rats line their sleeping quarters with leaves that kill flea larvae. Many species also avoid contact with faecal matter. For example, jackdaws and some tits carry faeces away from their nests (Lorenz, 1970) and many animals defecate away from their normal living sites (Grier, 1984). Additionally, great tits avoid parasitized nest sites (Merila & Allander, 1995).

The following experiments examined faecal avoidance behaviour in the unisexual gecko, *L. lugubris*, and the bisexual gecko, *H. frenatus*. The experiments were designed to examine whether the presence of faeces influenced the selection of daytime hiding places and whether the species avoided defecating near their daytime hiding places. We hypothesized that the unisexual and bisexual species would differ in the number and types of their faecal avoidance behaviours which would account for some of the differences in intestinal parasitism rates displayed by the two species.

METHODS

The first series of experiments was conducted to determine whether geckos chose daytime hiding places that were surrounded by sphagnum moss contaminated with faeces, or free from faeces (uncontaminated). Twenty *L. lugubris* and 18 *H. frenatus* were used as subjects in Experiment 1. Aquaria (51 x 28 x 31 cm) served as testing chambers. A small platform (8.5 x 3.5 cm) was placed at each end of every aquarium. These platforms simulate the characteristics of naturally occurring hiding places and are readily used by wild-captured geckos. One platform was surrounded by clean sphagnum moss and the other by sphagnum moss that had been used as bedding in an enclosure housing at least three geckos for a period of two months. Placement of moss as well as species of gecko were counterbalanced across aquaria. When an aquarium was reused, the uncontaminated/contaminated moss was placed on the opposite side and a different species of gecko was used as the subject (all aquaria were sanitized between experimental runs).

A geckos in an open bottle was placed in the middle of the aquarium (half way between the two platforms) in the afternoon. The next morning the position of the gecko was noted (i.e. in the bottle, on top of or inside a platform, or in the sphagnum moss). In addition, 10 of the above *L. lugubris* and nine of the *H. frenatus* were observed every 5 min for the first 90 min after they were placed in the aquarium. Observations were conducted to see whether the geckos used purely chemical cues in making their choices (in which case we hypothesized that they would not enter the contaminated moss) or tactile and chemical cues.

In Experiment 2, the platforms were surrounded by either dried faeces placed in an arc approximately 5 mm wide and 3 mm in depth or by nothing (34 L. lugubris and 28 H. frenatus were tested). In Experiment 3, the floor of the aquarium surrounding the platform was either sprayed with a solution of 15 ml ground dried faeces suspended in 300 ml distilled water or distilled water alone (50 L. lugubris and 52 H. frenatus were tested). The spray bottle containing the suspended faecal solution was vigorously shaken prior to each use. Gecko species and the placement of the stimuli were counterbalanced across the aquaria. All aquaria were sanitized prior to each use with a 1:1 bleach to water solution and were immediately wiped dry. Both experiments were conducted during the daytime. The geckos were placed in the aquaria between 8.00 and 9.00 am and positions of the geckos were noted 6 hrs later.

Experiment 4 examined whether or not geckos defecated near or away from their daytime hiding places. Ten *H. frenatus* (five females and five males) and 10 *L. lugubris* were housed individually in perspex enclosures ($32 \times 18 \times 23 \text{ cm}$). One small platform was centred along the back of each enclosure. Geckos were housed in the enclosures for a period of four days. Systematic observations (12 per day) were made of where each gecko was located within the enclosure to determine its preferred daytime hiding place. At the end of the four day period, the geckos were removed. Measurements were obtained on where each gecko defecated in relation to the gecko's most frequent daytime hiding place.

RESULTS

In Experiment 1, more geckos were found on the sides of the aquaria surrounded by uncontaminated sphagnum moss (13/17 *L. lugubris* and 11/15 *H. frenatus*) than on the contaminated sides (Fig. 1).

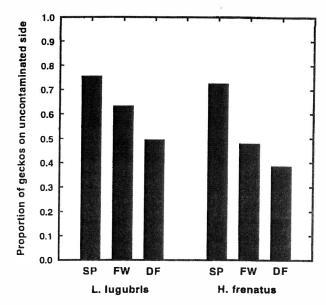


FIG. 1. Proportion of geckos that chose the uncontaminated side of the aquarium. SP refers to the geckos that were tested with sphagnum moss, FW to those tested with faeces mixed in distilled water, and DF to those tested with dry faeces.

When tested with χ^2 (corrected for continuity), the *L. lugubris* exhibited a significant preference for the uncontaminated moss and platform ($\chi^2 = 4.82$, df=1, *P* < 0.05), but *H. frenatus* did not ($\chi^2 = 3.33$, df=1, 0.05 < *P* < 0.10), perhaps due to the small sample size. Six geckos (three *L. lugubris* and three *H. frenatus*) were found in the bottles or at the top of the aquarium; these animals were not included in the analysis.

Of the geckos which were examined in greater detail, one gecko of each species did not leave the bottle during the 90 min, five geckos moved to either the uncontaminated side (n = 3) or to the top of the aquaria (n = 2) and remained there, and 10 geckos explored the aquaria more thoroughly. Eight moved to the contaminated side of the enclosure and then alternated back and forth between the sides, and two geckos moved to the uncontaminated side and then alternated. Of these 10

TABLE 1. The behaviours geckos displayed when they were observed every 5 minutes for 90 minutes in Experiment 1. Bottled geckos were placed between two platforms, one surrounded by clean sphagnum moss (uncontaminated), the other by sphagnum moss that contained gecko faeces (contaminated).

Behaviour	Species of Gecko	
	L. lugubris	H. frenatus
Remained in bottle	1	1
Moved to an uncontaminated		
area and remained	4	1
Moved to the uncontaminated		
side and alternated sides	1	1
Moved to the contaminated		
side and alternated sides	3	5

geckos, eight were found the next morning on the uncontaminated side of the aquarium and two on the contaminated side (Table 1).

Neither *L. lugubris* nor *H. frenatus* showed a preference for a particular side of the aquaria when dry faeces were used as stimuli in Experiment 2. Half of the *L. lugubris* (17/34) and 61% (17/28) of the *H. frenatus* were found on the platforms surrounded by dried faecal matter after 6 hrs (Fig. 1). In contrast, when faecal matter was in solution with distilled water (Experiment 3), *L. lugubris* displayed a significant preference for the platform sprayed with distilled water (32/50; $\chi^2 = 3.94$, df=1, *P* < 0.05) over the platform sprayed with faecal solution (18/50). *H. frenatus* did not display this preference (25/52 chose distilled water; Fig. 1). However, the difference between species was not significant ($\chi^2 =$ 1.52, df=1, *P* >0.05).

In Experiment 4, both species of gecko defecated away from their preferred daytime hiding places. *L. lugubris* defecated an average 22.6 cm from their hiding places and *H. frenatus* 13.2 cm. The difference between species was not significant ($F_{1,17} = 1.5, P > 0.05$).

DISCUSSION

Both the unisexual and bisexual gecko species defecated away from their preferred daytime hiding places, and when given a choice, preferred hiding places that were surrounded by faeces-free sphagnum moss. The unisexuals also avoided areas where faeces mixed with water had been sprayed, but neither species avoided crossing areas of dried faecal matter. A similar pattern is observed in geckos that inhabit man-made structures. After 12 years of observing nocturnal geckos, the senior author has never observed faecal matter near their daytime hiding places. Faecal matter accumulates, however, on ledges such as window casings. Ledges are crossed by geckos at dusk when the animals are climbing up to feed. Avoidance of faecal matter has been reported in birds (Lorenz, 1970) but has not, as far as we know, been reported before in a lizard species.

If contact with fresh faeces is more likely to spread disease than contact with dried faeces, then both gecko species appear to have evolved some ability to distinguish between fresh and dried faecal matter, avoiding the former and ignoring the latter. The unisexual L. lugubris is perhaps more sensitive to wet faecal matter than the bisexual H. frenatus, because the unisexuals avoided faecal water to a greater extent than bisexuals. Previously Hanley, Volmer & Case (1995) found that populations of L. lugubris in the Pacific Basin harboured fewer types of parasites and contained fewer infected individuals than H. frenatus. The fact that L. lugubris appears to be more sensitive to wet faeces might account for some of the differences in parasitism rates found between the species, although it does not rule out differences in innate immunity between the species.

Geckos of both species were more likely to explore both sides of the enclosure if they first entered the contaminated sphagnum moss. Thus, it does not appear that they are choosing the uncontaminated side of the enclosure via an air borne chemical. This finding supports Schwenk's (1993) hypothesis that geckos have poor vomeronasal senses. It could be that the geckos are using one of their skin sense organs (Matveyeva & Ananjeva, 1995) to make the choice and therefore have to have closer contact with wet faecal matter before avoiding it. Further research needs to be conducted on how the geckos choose an uncontaminated hiding place.

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REFERENCES

- Atkinson, C. T. & Van Riper III, C. (1991). Pathogenicity and epizootiology of avian haematozoa: plasmodium, leucocytozoon, and haemoproteus. In *Bird-parasite interactions*, 19-48. Loye, J. E. & Zuk, M. (Eds.). Oxford University Press.
- Brown, S. G., Kwan, S. & Shero, S. (1995). The parasitic theory of sexual reproduction: parasitism in unisexual and bisexual geckos. *Proc. R. Soc. Lond. B* 260, 317-320.
- Grier, J. W. (1984). *Biology of Animal Behavior*. St. Louis: Times Mirror/Mosby College Publishing.
- Hanley, K. A., Fisher, R. N. & Case, T. J. (1995). Lower mite infestations in an asexual gecko compared to its sexual ancestors. *Evolution* 49, 418-426.
- Hanley, K. A., Volmer, D. M. & Case, T. J. (1995). The distribution and prevalence for helminths, coccidia and blood parasites in two competing species of geckos: implications for apparent competition. *Oecologia* 102, 220-229.
- Hemmes, R., Alvarado, A., Cliff, K. & Hart, B. L. (1995). Nest fumigation behavior in a mammal: evidence that the dusky-footed wood rat uses California bay leaves to control nest-borne ectoparasites. *Paper presented* at the meeting of the XXIV International Ethological Conference, Honolulu, HI.
- Lorenz, K. (1970). Studies in Animal and Human Behaviour. Cambridge: Harvard University Press.
- Matveyeva, T. N. & Ananjeva (1995). The distribution of the skin sense organs of agamid, iguanid and gekkonid lizards. J. Zool., Lond. 235, 253-268.
- Merila, J. & Allander, K. (1995). Do great tits (*Parus major*) prefer ectoparasite-free roost sites? An experiment. *Ethology* 99, 53-60.
- Radtkey, R. R., Donnellan, S. C., Fisher, R. N., Moritz, C.& Case, T. J. (1995). When species collide: the origin

and spread of an asexual species of gecko. Proc. R. Soc. Lond. B 259, 145-152.

- Rodriguez, E. & Wrangham, R. (1993).
 Zoopharmocognosy: The use of medicinal plants by animals. In *Phytochemical Potential of Tropical Plants*, 89-105. Downum, R. R., Romeo, J. T. & Stafford, H. A. (Eds). New York: Plenum Press.
- Schwenk, K. (1993). Are geckos olfactory specialists? J. Zool. Lond. 229, 289-302.
- Seger, J. & Hamilton, W. D. (1988). Parasites and sex. In The Evolution of Sex, 176-193. Michod, R. E. & Levin B. R. (Eds). Sunderland, Massachusetts: Sinauer Associates Inc.

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