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The tortoise and the rail

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Giant tortoises (*Geochelone gigantea*) on Aldabra respond to light tactile stimulation of their soft posterior regions by adopting an immobile erect stance, previously thought to be a threat posture. It is argued that this is probably a cooperative posture assisting any potential symbiont to clean ectoparasites from the areas of soft skin thus exposed. Most Aldabran tortoises over 25 cm long respond in this way and the response appears to be unaffected by activity, sex, time of day and ectoparasite abundance. The visual stimulus of a white-throated rail *Dryolimnas cuvieri* within 1 m may also elicit this response, and rails were observed removing ectoparasites from tortoises which had adopted the cooperative posture. The distributions of the tortoise and the rail overlap only slightly and the mutualism is thought to be ecologically unimportant to both the ectoparasites and the rail. Comparisons are made with the mutualism involving Galápagos giant tortoises, *Geochelone elephantopus*, and the ground finches *Geospiza fuliginosa* and *G. fortis*, and the mockingbird, *Nesomimus parvulus*.

1. Introduction

Frazier (1972) reported that light tactile stimulation, especially of the areas of softer skin at the posterior end, usually evokes a response in the Aldabran giant tortoise, *Geochelone gigantea*, in which the neck and limbs are extended so that the body is lifted well clear of the ground (see figure 1). He called this the 'standing' posture, but was unsure of its function or cause. He had observed that it occurred during sequences of mating behaviour, and concluded that it was adopted in situations of behavioural conflict, and seemed to be a threat posture. MacFarland & MacFarland (1972) discovered a mutualistic relation between the giant tortoises of the Galápagos (*Geochelone elephantopus*) and the ground finches *Geospiza fuliginosa* and *G. fortis* in which the finches 'cleaned' the tortoise of ectoparasitic ticks. This relation was described in some detail (MacFarland & Reeder 1974) and included the adoption of a cooperative ('extended') posture by the tortoise which bore a marked resemblance to Frazier's (1972) 'standing' posture. Rodhouse *et al.* (1975) also reported this behaviour, but added the involvement of the mockingbird, *Nesomimus parvulus*. Previous descriptions of a supposed mutualistic relation involving the Aldabran giant tortoises have concerned the diurnally active gecko, *Phelsuma abbotti*, which was seen feeding on *Aedes* mosquitoes attracted to the tortoises (Honegger 1966; Stoddart & Wright 1967), but did not include the tortoise's assumption of a cooperative posture.

This paper attempts to explain the derivation of the 'standing' posture of Aldabran giant tortoises, and describes a mutualistic relation between giant tortoises and the Aldabran white-throated rail, *Dryolimnas cuvieri aldabranus*, in which the tortoise assists the rail in its cleaning rôle by assuming a cooperative posture.

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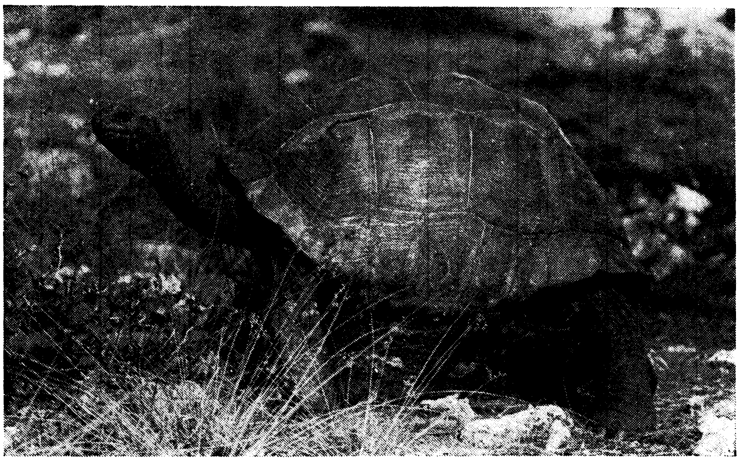

FIGURE 1

2. METHODS AND STUDY AREAS

(a) *Tactile stimulation*

Tortoises were tested in December 1975 and January 1976 for response to light tactile stimulation, on Ile Malabar (mostly near Passe Houareau) and on Grande Terre at and near Dune Jean-Louis. Each tortoise was approached quitely from behind so that the observer remained apparently undetected. If the animal became aware of the observer, it would either move off rapidly or retract into its shell and was not included in the results; if it remained undisturbed the back legs were scratched lightly in the thigh region with a thin wooden stick for 30 s. The response was noted, as was the tortoise's activity before approach and stimulation, and its position relative to direct sunlight or shade. The number of ectoparasites (tabanid flies and mosquitoes, see §3*b* below) present was estimated during stimulation and classified as nil, few (up to 5) or many (over 5). Finally, the tortoise was sexed (where possible) and measured (carapace straight length in centimetres). The responses were grouped into three categories; positive, in which the animal adopted the 'standing' posture, negative, in which the animal either moved off, retracted into its shell or adopted the 'protected' posture (Frazier 1972) with the rear end lowered to the ground, or no response, in which the animal apparently ignored the stimulus.

(b) *Visual stimulation*

Undisturbed tortoises were observed in December 1975 and January, February and March 1976 on Ile Malabar and Grande Terre (at Cinq Cases and Dune Jean-Louis), and any interactions with other animals passing within 1 m in front of the tortoise were noted. Responses were categorized as in §2*a* above.

3. RESULTS

(a) *The posture*

It is assumed that the cooperative posture described here is identical to Frazier's (1972) 'standing' posture, and may occur as a response to certain visual stimuli, light tactile stimuli and also during sequences of attempted mating, although in this last case the stimulus is probably tactile. The four limbs are extended more or less fully so that the plastron is well clear of the ground, and the neck is stretched out nearly vertically, horizontally or in an intermediate position (figure 1). One important characteristic of this posture is that once it is adopted the tortoise remains motionless, appearing to be in an almost trance-like state, and may ignore other stimuli that would normally elicit an avoidance response. Extension of the four limbs may be either synchronous or asynchronous, but if it is asynchronous the first limbs to be extended are usually those nearest the stimulus. There was no apparent difference between the posture adopted in response to visual cues and that adopted in response to tactile stimulation, and the 'extended' posture of the Galápagos tortoises seems to be more or less identical (MacFarland & Reeder 1974; Rodhouse *et al.* 1975). Maintenance of the posture may continue for some time (up to at least 2 min) after cessation of either form of stimulation.

Table 1. Response of tortoises to tactile stimulation

locality	number of positive responses	number of negative responses	no response	
Ile Malabar	48 (79 %)	13 (21 %)	0	61
Grande Terre (Dune Jean-Louis)	69 (93 %)	3 (4 %)	2 (3 %)	74

(*b*) *Ectoparasites*

Aldabran tortoises appear not to carry any ticks, unlike those in the Galápagos which support large numbers of *Amblyomma usingeri* and *Argas transversus*. However, mosquitoes (probably *Aedes* sp.) frequently occur in considerable numbers on and around Aldabran tortoises, and the tabanid flies *Neavella albipectus* and possibly *Aegophagamyia remota* are also commonly present. Both the mosquitoes and the flies tend to congregate around the areas of soft skin on the neck, legs and between the plastron and carapace. The tabanids are also seen on the carapace. It is not known how much the biting activity of these insects affects the tortoises' behaviour.

(*c*) *Response to tactile stimulation*

Most tortoises responded positively to tactile stimulation (table 1). The results were examined to determine whether the tortoises' activity and position affected their response, but there was no such effect. Nor was the response related to the number of mosquitoes and flies present, or the time of day. Both sexes responded more or less equally (males, 50 out of 60 = 83 % positive; females, 63 out of 71 = 88 % positive), and size appeared to have no effect, except that three very small tortoises (i.e. less than 25 cm straight length) tested separately all responded negatively.

In one instance a tortoise was seen to adopt the cooperative posture in response to tactile stimuli under natural conditions. The tortoise, which was feeding, was approached from the rear by a rail which was not visible to the tortoise. The rail began to peck at and around the back legs of the tortoise which immediately assumed the cooperative posture. The rail moved off after a few seconds and the tortoise lowered itself 15 s later and resumed feeding.

(*d*) *Response to visual stimuli*

Other than instances involving rails, detailed observations were made of tortoises' behaviour on 44 occasions when another animal passed in front of, and within 1 m of, an active (i.e. not sleeping) tortoise. The results are shown in table 2 from which it can be seen that tortoises normally make no response at all. On one occasion a tortoise briefly adopted the cooperative posture in response to a foraging turnstone (*Arenaria interpres*); the latter ignored the tortoise which lowered itself after a few seconds. Of the 19 instances involving rails (table 2), in only one was there no response, and in the other 18 positive responses occurred; these are described in detail in §3*e* below.

TABLE 2. RESPONSE OF NON-SLEEPING TORTOISES TO PRESENCE OF OTHER ANIMALS WITHIN 1 m AND WITHIN VISUAL RANGE

animal	area	number of positive responses	number of negative responses	no responses	total number studied
robber crab, *Birgus latro*	Ile Malabar	0	1	5	6
land crab, *Cardisoma carnifex*	Ile Malabar (5) Grande Terre (13)	0	0	18	18
sacred ibis, *Threskiornis aethiopica*	Grande Terre	0	1	4	5
turnstone, *Arenaria interpres*	Ile Malabar	1	0	3	4
turtle dove, *Streptopelia picturata*	Ile Malabar	0	0	11	11
white-throated rail, *Dryolimnas cuvieri*	Ile Malabar	18	0	1	19

(*e*) *Tortoise/rail interactions*

Tortoises responded rapidly to the sight of a rail within 1 m. Both males and females exhibited this response, and their sizes ranged from 49 to 80 cm straight length. The one animal (female) that did not respond was 64 cm straight length. In nine instances the rail apparently ignored the tortoise's assumption of the cooperative posture; on five occasions the bird showed some interest in the tortoise, but did not feed or attempt to feed on the tabanid flies and mosquitoes present, foraging instead in the disturbed area around the tortoise. However, in the remaining four instances the rail was seen to 'clean' the tortoise, searching the legs, neck and areas of exposed skin in the space between the plastron and the carapace, and in one case the bird actually pecked inside the nostrils of the tortoise, the latter seemingly unaffected by this, other than a slight retraction of the head. Rails were seen to take both tabanid flies and mosquitoes while 'cleaning' a tortoise. It should be stressed here that the presence of a human observer may have considerably affected the rails' behaviour towards the tortoises. Several of the rails observed in interactions with tortoises showed greater interest in the observer than in the tortoise.

Only adult rails were seen to be involved in cleaning behaviour, but on one occasion a 9 week old juvenile elicited the response in a tortoise and then investigated the latter's front legs, but did not attempt to take any of the tabanid flies or mosquitoes present.

4. DISCUSSION

Frazier (1972) concluded that the posture he described as 'standing' was involved in sexual behaviour, but admitted that its function and cause were not at all clear. It is suggested here that when 'standing' occurs in a sequence of mating behaviour it is out of context and that the response is elicited in these instances not by the approach of another tortoise but by light tactile stimulation. Frazier noted that 'standing' occurred in the early stages of mating behaviour and he reported that it is during these phases that the male tortoise 'noses' the partner, normally approaching from the rear. Thus it seems possible that the tortoise being 'nosed' mistakes the sexual approach of the other and adopts the cooperative posture out of context. There seems little doubt that the posture adopted in these circumstances was identical to the cooperative posture adopted when a rail approached, especially in view of the one observation of a tortoise assuming the posture in response to tactile stimulation from an unseen bird (see §3*c*). The evidence also points to its not being an aggressive posture since, at least in the Galápagos tortoise, this latter usually involves face to face confrontations and considerable movements of the head, neck and sometimes the legs (MacFarland & Reeder 1974). Frazier's explanation that it is a threat display elicited in a state of behavioural conflict is therefore superfluous if one accepts that it is a behaviour pattern occuring out of context in response to simple tactile stimuli. This argument is supported by the almost universal response of tortoises to experimental tactile stimulation, and the apparent lack of any factors affecting the response rate.

That this is a ritualized posture seems likely, but its origins are not clear. It may have derived from an intention movement in which the tortoise extended its limbs before locomotion, or it may have originated in the autonomic response sometimes involved in defecation (Frazier 1972) in which the hind legs only are extended, lifting the posterior clear of the ground. In either case, the exaggeration of the posture may be considered as ritualization and it is clearly functional in exposing the maximum possible area of soft skin for inspection by any mutualist. There is a third explanation for which I am indebted to H. Fricke (personal communication). He has observed a similar posture in the small Greek tortoise *Testudo graeca* and believes it to be a comfort posture; if this were the case, ritualization need not be involved, and the evolution of a mutualistic relation would be much simpler to envisage.

The Galápagos tortoises adopt the cooperative posture in response to approach either by the ground finch or the mockingbird, or to a special 'presentation' display by the ground finch (MacFarland & Reeder 1974; Rodhouse *et al.* 1975). In contrast, the Aldabran tortoises respond only to approach by a rail, and there is no apparent display by the bird. It is suggested here that the tortoise's response to the sight of a rail is learned (as is the rail's response to a tortoise in the cooperative posture), and it would be of interest to test the response of Aldabran tortoises that have never encountered a rail, such as those on Grande Terre. It is also possible that the Galápagos tortoises respond to a call given by the mockingbird (Rodhouse *et al.* 1975), but this seems less likely in view of their probably poor auditory acuity (Frazier 1972). However, O. Prŷs-Jones has recently informed me (personal communication) that he has observed Aldabran tortoises adopting the cooperative posture apparently in response to auditory stimuli only, in this case rails singing out of sight of the tortoise concerned. It would be interesting to confirm this experimentally and to determine whether the tortoises respond to the whole song or just to the low frequency notes (Huxley & Wilkinson 1977) that are within their reported range of good auditory acuity.

Penny & Diamond (1971) reported rails taking tabanid flies from tortoise carapaces on several occasions, and although they also noted one instance in which a rail pecked at the head and front legs of a tortoise, in this case the tortoise responded negatively by withdrawing into its shell. The occurrence of rails foraging in the area of disturbed litter around a tortoise was also recorded by Penny & Diamond (1971), although they did not report observing the tortoises adopting the cooperative posture and likened the relation to that occurring between the cattle egret (*Bubulcus ibis*) and ungulates.

The density of tortoises on Ile Malabar is approximately 7 per hectare in the areas of open/mixed scrub, but nil in the *Pemphis acidula* scrub which covers most of this island (Bourn 1976). Thus, although those rails living in the open and mixed scrub habitats will encounter tortoises fairly frequently (a pair of rails generally holds a territory of 1–2 ha and will thus have up to about 15 tortoises available), the great majority of rails on Ile Malabar (probably in excess of 75% of the total population) will have little or no chance of meeting a giant tortoise. Less than 2% of the total population of tortoises on Aldabra live in areas inhabited by rails (Bourn 1976) and it is to be concluded, therefore, that the mutualistic relation described here is unimportant to the tortoise population as a whole. The mobility and abundance of tabanid flies and mosquitoes is such that it is unlikely that even in the areas where the mutualism occurs the rails have any significant effect on their numbers. This contrasts with the situation in the Galápagos where MacFarland & Reeder (1974) found that cleaning by the finches resulted in a marked decrease in the abundance and distribution of partly to fully engorged *Amblyomma* ticks. It is not thought that the amount of food collected by rails from tortoises forms a significant part of their diet since the proportion of their time spent in this behaviour is negligible, and in this respect the relation again differs from that in the Galápagos where ticks taken from tortoises may form an important part of the finches' diet at certain times of year (MacFarland & Reeder 1974).

It appears that the relation between Aldabran tortoises and rails is a rather casual one, possibly in its evolutionary infancy, in which both species benefit, but not to any important extent. Its importance and interest lie, then, not in the ecological aspects but in the behavioural implications.

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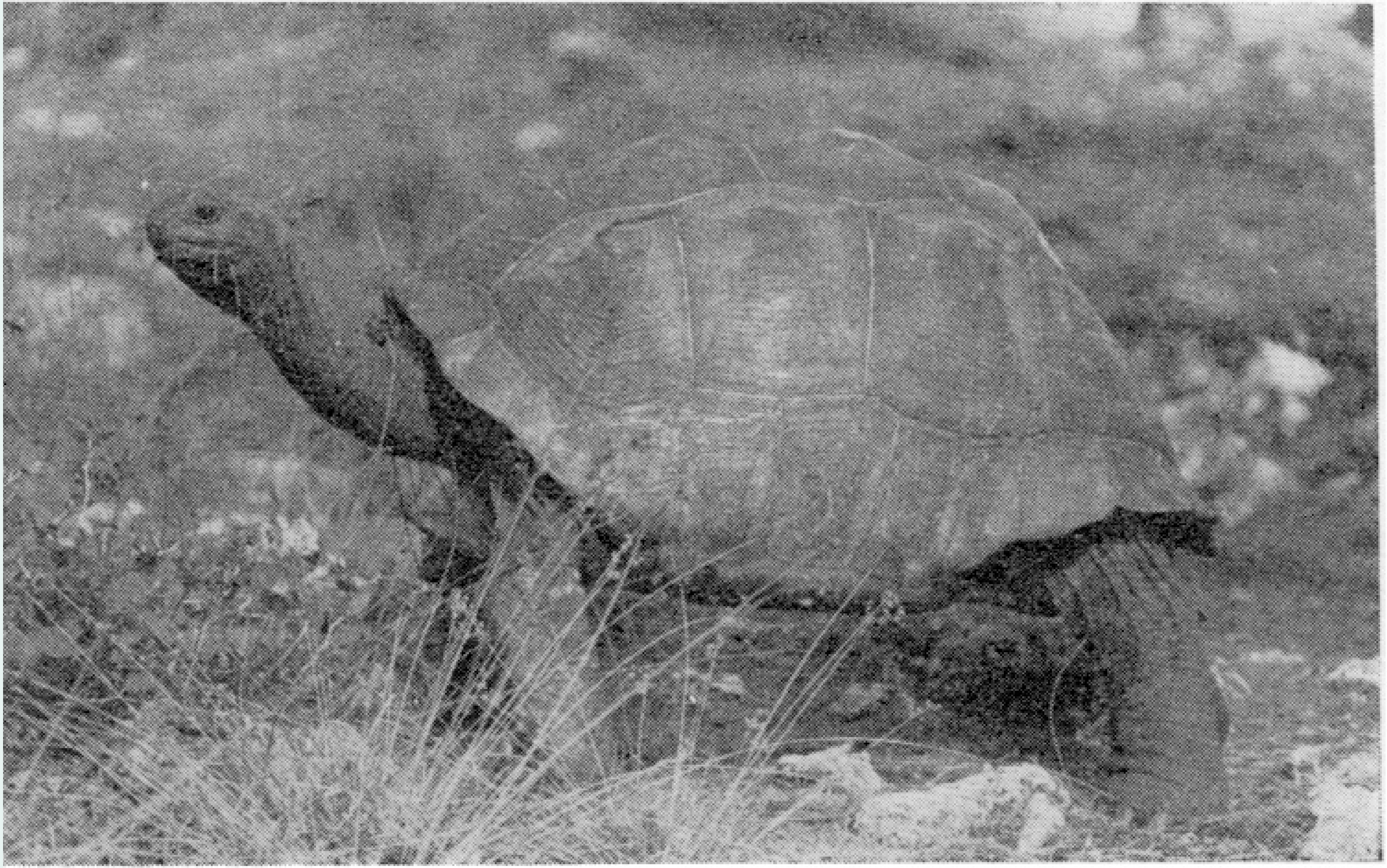

Figure 1