shown elsewhere[18] that for smaller islands lizards frequently jump into the sea, possibly to swim or drift to another island.

Successful colonization of most islands not having lizards naturally shows that chronic factors, such as desiccation of eggs or adults, or starvation, cannot be agents of extinction. Perhaps populations will eventually overeat their food and crash; however, severe oscillations are theoretically unlikely in systems such as ours where much food 'drifts' in from elsewhere[19], and our numbers give no evidence of them. Several lines of evidence (refs 4, 5, 19, manuscript in preparation), of which the above results comprise only one, imply that minimal areas supporting lizard populations reflect 'bottlenecks' caused by periodic catastrophies, in this case especially destructive hurricanes. Our hypothesis, aspects of which we are now testing experimentally, is that hurricanes cause not only much short-term mortality, but also long-term devastation of the vegetation and concomitant resource shortage. During the aftermath of a hurricane, populations of lizards go extinct on islands that, once their vegetation has recovered, could support them, sometimes lavishly. For this explanation to hold, immigration during favourable times must be virtually nil; indeed, we also hypothesize that immigration is pulse-like in this system, occurring during and immediately following a hurricane, when lizards are especially likely to be in the water. In short, we suggest that present-day distributions of lizards on small islands are in several senses the high-water marks of past disasters.

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Polyandry, cloaca-pecking and sperm competition in dunnocks

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A variety of behaviours adopted by males before and after copulation serve to increase paternity. The most spectacular examples occur in insects where males increase their own chances of fertilizing the female's eggs by mate guarding, mating plugs and even removal of other males' sperm[1,2]. Here, sperm competition is described for a small European passerine bird, the dunnock (*Prunella modularis*), where females are often mated simultaneously to two males[3,4] and where there is an elaborate pre-copulatory display[5,6]. It is shown that, during this display, the male stimulates the female to eject sperm before he himself copulates. The display is most intense where there is a high probability that another male has recently mated with the female.

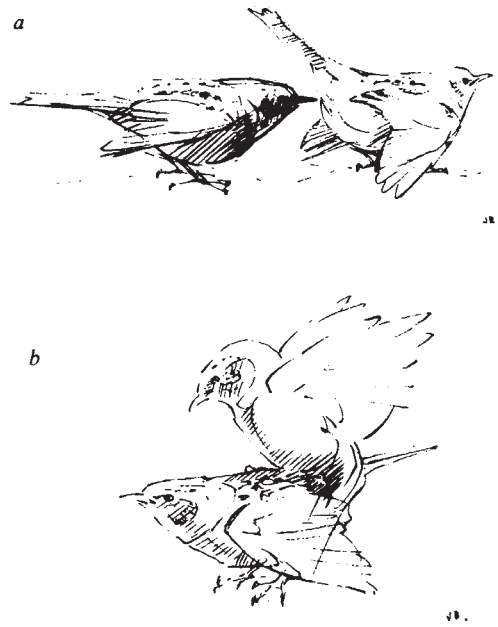

Fig. 1 *a*, The male first stands behind the female and pecks her cloaca. Mean duration of display was 50.2 s, range 5–120 s. Mean number of pecks was 27.9, range 0–118 pecks; 74 displays observed. *b*, Then he copulates. Copulation itself is very brief, the male appears to jump over the female, cloacal contact lasting for just a fraction of a second. (Drawing by John Busby).

The study site is the Cambridge University Botanic Garden where, at the start of the breeding season in 1982, there was a colour-ringed population of 48 males and 31 females. The male-biased sex ratio is probably a consequence of greater female mortality during winter. Females are smaller than males, subordinate at feeding sites and more likely to die or leave temporarily when competition for food is intense. The mating combinations on some of the breeding territories were very complicated but the commonest situations were either a monogamous pair (10 territories) or a trio with two males (not close relatives) associating with the same female (15 territories). In trios, one of the males, the alpha male, was dominant to the other, the beta male, both at feeding sites and over access to the female. Alpha males (mean wing length 70.5 mm) were significantly larger than beta males (mean 69.3 mm, $P < 0.02$).

Monogamous males and alpha males of trios began to follow the female closely, mainly staying within 5 m of her, 4 to 5 days before she laid her first egg, similar to the onset of mate guarding in other species[7]. Neighbouring males often encroached onto the territory and attempted to copulate with the female but by far the most intense competition occurred between the males of a trio. Here the beta male constantly approached the female and the alpha male spent up to 30 min per h chasing him away. There were often fights and in two cases the beta male was blinded in one eye and subsequently died.

Mate guarding behaviour was studied in detail for 25 breeding attempts, including first and second broods in 1981 and 1982 (data from 19 different territories). The female on each of these territories was watched continuously for 1–3 h daily during the mating period. In three of the four breeding attempts by monogamous pairs, only the resident male was seen to mate while in the other case a trespassing neighbour also mated with the female. Of the 21 breeding attempts by trios, only the alpha male was seen to copulate in 12 cases, while in the other 9 both alpha and beta male copulated. Beta males sometimes managed to approach the female and copulate without the alpha male noticing, for example when he was busy feeding or out of sight on the other side of a bush. On other occasions the alpha male lost the female temporarily after chasing the beta male. If the beta male was then the first to find the female again he was able to mate with her unhindered.

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In most passerine birds the preliminary display immediately before copulation is very brief. In dunnocks by contrast, it is an extraordinarily elaborate affair. The female crouches, fluffs up her body feathers, shivers her wings and quivers her tail which is raised to expose the cloaca. The male hops from side to side behind her and pecks her cloaca for up to 2 min before he copulates (Fig. 1). Monogamous males and both alpha and beta males of trios pecked the female's cloaca before they mated.

During the pecking by the male, the female's cloaca becomes pink and distended and from time to time makes strong pumping movements. As the cloaca contracts the female jerks her abdomen downwards and sometimes is seen to eject a small pale mass. (There is one previous report[8] of a female ejecting a 'small drop of fluid' during the cloaca contractions.) A small droplet was found on three occasions by careful search of the ground where a male and female had been displaying, and examination of the droplets through a microscope revealed them to be sperm masses (Fig. 2). One of the sperm masses was extruded together with a small amount of faecal material. On 11 other occasions the female extruded larger pellets during the pre-copulatory display and these were all confirmed to be faecal pellets only. It was impossible to see whether the female ejected something during every display and because the sperm droplets were so small it is possible that others were deposited but not found. The male sometimes pecked at the ejected mass and in all five cases where the display sequence was seen in close detail, he copulated with the female immediately after she had produced the deposit.

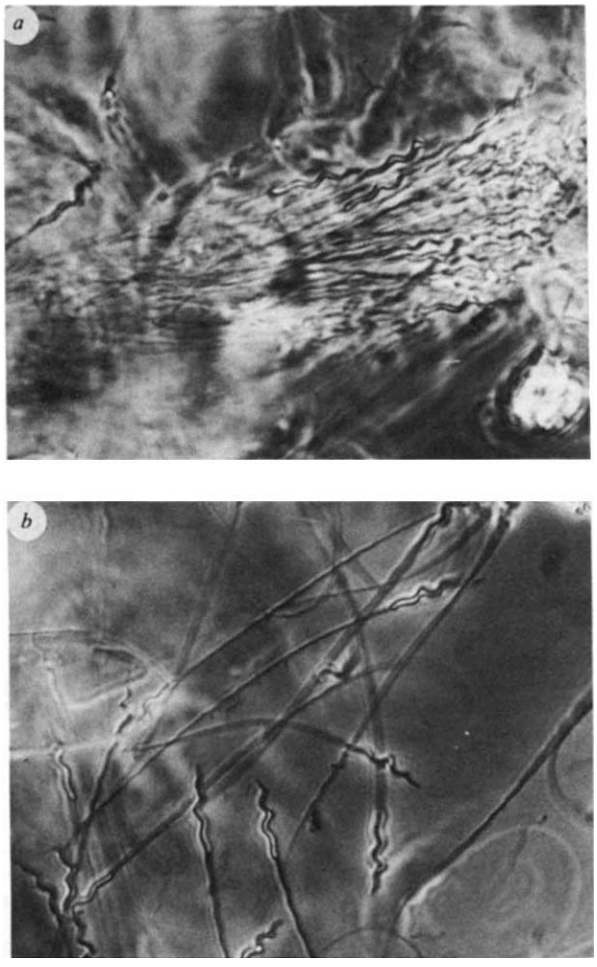

Fig. 2 *a*, Part of a sperm mass ejected by the female during cloaca pecking by the male. The semen of passerine birds is a small glutinous droplet, with little accessory fluid, containing bundles of sperm, which have helical heads[13]. *b*, Some individual sperm on the edge of the mass.

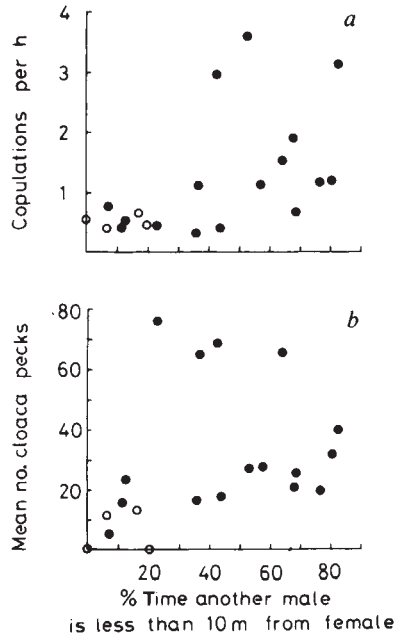

Fig. 3 *a*, Males copulate more frequently when they are with the female (less than 10 m) the greater the proportion of time another male spends close to her. Open circles are data from 4 monogamously paired males where 'other males' are trespassing neighbours. Closed circles are 16 alpha males of trios where most of the interference is by beta males resident on the territory (Spearman rank correlation on all points is 0.627, $P<0.01$; on alpha males data only, it is 0.582, $P<0.05$. *b*, Males also peck the female's cloaca more each time before they copulate the more time another male spends close to her (Spearman rank correlation on all points is 0.598, $P<0.01$; on alpha male data only, it is 0.300, NS).

In birds, it is thought that the male ejaculates sperm into the female's vagina which is a short muscular duct joining the cloaca[9]. There are sperm-host glands in the utero-vaginal junction where the sperm is stored for some time before it is transported up to the top of the oviduct where fertilization takes place immediately after ovulation, about 24 h before the egg is laid[9–11]. The egg has to be fertilized during its brief sojourn in the infundibulum, a period of only 15–30 min. It is unlikely that the female can be certain of copulating during this brief period which presumably explains why sperm is stored and then moved up the oviduct just before ovulation so as to be available at the critical time for fertilization[11].

One hypothesis for the cloaca-pecking by the male is that it stimulates the female to eject sperm likely to have been inseminated by another male. Any strong contractions in the female's urogenital tract would presumably eject faeces as well if any were in the cloaca at the time. In accord with this sperm competition hypothesis, a male both copulates more frequently and does more pecking in each pre-copulatory display the more time another male spends near his female (Fig. 3). In trios the proportion of time a beta male spends within 10 m of the female is negatively correlated with the alpha male's wing length (Spearman rank correlation -0.776, $P<0.01$, $n=13$), which suggests that larger alpha males are better able to monopolize exclusive access to the female and keep beta males at bay. Monogamous males are even larger than alpha males of trios and are able to evict beta males out of their territories altogether (manuscript in preparation).

One of the presumed costs of a long pre-copulatory display is a high probability that a male will be interrupted by another male before he actually copulates. Fifty out of 125 copulation attempts by alpha males were interrupted during the cloaca-pecking by a beta male's arrival, whereupon the alpha male left the female to chase him. Fourteen out of 38 attempts by beta males were interrupted by the alpha male. The advantages of cloaca-pecking must be considerable to offset this cost. The

details of sperm competition are not known for any wild bird but one possibility is that if the female's sperm store becomes full then the only chance a male has of putting sperm in himself is to remove sperm first to make room. Even if the store is not full, however, it may pay a male to risk the cost of interruption in order to remove sperm which might not be his and insert sperm which he can be certain is his own.

It would be difficult to tell from field observations exactly how often a female ejects sperm but it is interesting to speculate on the possible advantage to her of doing so. One possibility is that it is a mechanism by which she increases the chances that her clutch of eggs is fertilized by more than one male. Females actively attempted to escape the guarding of the alpha male and often approached the beta male to solicit copulations. In all seven cases where both alpha and beta male copulated with the female and chicks were hatched successfully, both males fed the brood. By contrast, the beta male never fed the brood in the five cases where chicks hatched and only the alpha male had mated. Nestlings fed by two males get more food, fledge at a heavier weight and survive better than those fed by just one male (manuscript in preparation). Females can therefore increase their reproductive success if they get both males to fertilize their clutch or indeed persuade them both that they have some paternity[12].

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Magnetic particles in the liver: a probe for intracellular movement

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Previous studies have used magnetic particles to estimate the viscosity of cell cytoplasm *in vitro*[1–4]. Here we describe how magnetic Fe_2O_3 particles can be used to estimate non-invasively the motion of organelles in hepatic macrophages in intact animals. We report that when these particles are injected intravenously (i.v.), most are phagocytosed by hepatic macrophages (Fig. 1)[5]. When an external magnetic field is applied to the rabbit, these particles become magnetized and aligned. After removal of the field, the particles collectively produce a remanent magnetic field which can be measured at the body surface. This field decreases with time due to particle rotation (relaxation)[6,7]. As the particles are contained in phagosomes or secondary lysosomes, we conclude that motions of these organelles are responsible for the particle rotation and relaxation.

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Submicrometric γ-Fe_2O_3 particles[8] (2 mg suspended in 1 ml physiological saline) were injected i.v. into four adult male New Zealand White rabbits. For each measurement of relaxation, the rabbits were anaesthetized with 50 mg kg^{-1} ketamine-HCl given intramuscularly and then placed in a 60-mT magnetic field for 5 min. This time is adequate to magnetize all the particles and align them with the external field. To measure the gradual decay of the remanent magnetic field, the rabbit was placed inside a cylindrical moly-permalloy shield and its xiphoid process (a reliable reference point for the liver) repeatedly presented to a fluxgate magnetometer probe (Magnetoscop F 1.067; Foerster Instruments, Pennsylvania). This procedure was continued for 30 min. Magnetizations and relaxation measurements were performed at 2 h, and 1, 2, 3 and 4 days after particle injection. To prevent magnetic contamination of the animals, they were kept in non-ferrous cages and fed only fresh vegetables and water; commercial rabbit food was found to contain magnetic contaminants.

After the final measurement on day 4, each animal was killed and the amount of magnetic material in the liver, spleen, lung, heart and stomach was determined by magnetizing a tissue sample from each organ and measuring its remanent field with the fluxgate magnetometer. More than 90% of the retained γ-Fe_2O_3 was found in the liver, some in the spleen, but only minute amounts in other organs. Samples of liver and spleen were examined by light and electron microscopy. Abundant iron oxide particles were observed in phagosomes and secondary lysosomes of Kupffer cells (Fig. 1); no particles were seen in any other cell type in the liver. Some particles were also found in splenic macrophages.

Table 1 Relaxation rate for the first minute of measurement, λ_0

Day	λ_0(min^{-1})
0*	0.408 ± 0.120†
1	0.357 ± 0.067
2	0.341 ± 0.138
3	0.262 ± 0.044
4	0.264 ± 0.068

* Actual time of measurement was 2 h after injection.
† Decrease of λ_0 with time is significant at $P < 0.02$, by analysis of co-variance. The means are shown with their standard deviations.

Figure 2 shows a relaxation measurement demonstrating the progressive decrease of the remanent field after removal of the external field. This reflects the gradual misalignment of the magnetized particles. As it took 10 s to move the animal from the magnetizing field to the shielded magnetometer probe, we estimated the initial remanent field strength, B_0, by fitting the data to an exponential equation as suggested by Cohen *et al.*[9] and extrapolating back to time zero. This equation, $B = B_0 e^{-\lambda_0 t}$ (where B is the field strength at time t) also allowed us to describe the rate of decay during the first minute, λ_0.

During the 4 days of observation, B_0 (proportional to the amount of iron oxide present) did not change significantly; we conclude that there was negligible loss of particles from the liver during this time. The parameter λ_0, however, decreased significantly (Table 1), showing that the process of particle misalignment gradually slowed. There was also a significant slowing during the remaining portion of each relaxation curve, but to a lesser degree. We also found that relaxation ceased shortly after the animal was killed on day 4 (Fig. 3); for about 6 min after the heart stopped beating, relaxation continued, then further particle rotation within the Kupffer cells stopped as indicated by a constant remanent field. When the animals were placed in a magnetizing field between 10 and 60 min after death, no relaxation was observed, although the same initial field (B_0) was produced.

This is the first demonstration of relaxation in an organ other than the lung. Relaxation of magnetic particles was first noted in the lungs of welders by Cohen[6], and there have been additional reports of this phenomenon in other human[7,9,10] and

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