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Long-term decreases of corticosterone in captive migrant shorebirds that maintain seasonal mass and moult cycles

Theunis Piersma and Marilyn Ramenofsky

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Two flocks of Red Knots *Calidris canutus*, belonging to the temperate-wintering subspecies *islandica* and to the tropical-wintering subspecies *canutus*, were kept in outdoor cages at north-temperate latitudes over two annual cycles during which their plasma concentrations of corticosterone were measured at 4–6 week intervals. *Islandica*-knots maintained the schedules of moult and body mass changes of their counterparts in the wild over the two years of study, but *canutus*-knots showed deviations from normal annual rhythms. Even though the range of measured corticosterone concentrations was great, values remained well within those measured in free-living shorebirds. As predicted on the basis of past research, plasma corticosterone increased with respect to time required to capture and handle the birds during each sampling episode (capture-stress response). Plasma concentrations of corticosterone were also somewhat greater during spring migration periods (when birds had higher than average body masses) than at other times. In the *islandica*-, but not the *canutus*-flock, there were significant differences between individual concentrations of corticosterone. However, even after taking the foregoing factors into account, for the group showing the most natural mass and moult cycles (*islandica*), by far the strongest effect on corticosterone concentrations was the time since being taken into captivity. The longer the birds had been in the artificial aviary-environment, the lower the concentrations of plasma corticosterone became. Long-distance migrant bird species such as Red Knots normally encounter a wide range of environments during the course of their annual cycle. We interpret the long-term decrease in corticosterone in the light of its role in mediating appropriate physiological responses of birds faced with ecological variability in their environment and the occurrence of unpredictable events. We hypothesize that only after experiencing a full annual cycle in captivity do such birds recognize captive conditions as normal and as predictable.

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Birds and other animals display spatial movements to varying degrees (Baker 1978, Alerstam 1990, Dingle 1996). These movements may be confined to a single habitat, but may also involve long-distance migrations ranging from tens to thousands of km encompassing a wide variety of habitats, as is the case for many avian migrants such as the Red Knot *Calidris canutus* (Piersma and Davidson 1992, Harrington 1996). The latter type of movements occur biannually throughout an individual's lifetime and have been considered 'regu-

lar' or 'predictable' (Wingfield and Ramenofsky 1997). Yet, unpredictable conditions may disrupt the normal progression of events involving feeding, resting, and flying, thus increasing the demands for energy. Such conditions may include severe storms at a stopover site or strong headwinds en route. Faced with such predicaments, birds will attempt to cope with the unpredicted (and intolerable) situation, displaying appropriate behavioural responses termed 'facultative' (Wingfield et al. 1990, Wingfield and Ramenofsky

1997). But how do birds decide that a condition is intolerable? Perhaps they somehow compare present conditions (observed) with those that are previously experienced or, for naive individuals, endogenously predicted (expected). Alternatively, but not exclusively, they discern alterations in demand for, and supply of, energy (or nutrients). Thus, environmental conditions of a given habitat, whether natural or artificial, or a change in energy flux may influence physiology and subsequent behaviour.

Endocrine mechanisms implicated in decisions associated with facultative behaviour involve the adrenal corticosteroid, corticosterone (Wingfield 1994, Hahn et al. 1995, O'Reilly and Wingfield 1995, Wingfield and Ramenofsky 1997). Data on passerines (Rohwer and Wingfield 1981, Schwabl et al. 1985, Rogers et al. 1993) and seabirds (Smith et al. 1994) suggest that a change in the environment may trigger a response in the hypothalamic-pituitary-adrenal axis, resulting in an increase in plasma corticosterone. In turn, such increases in corticosterone may direct facultative behaviours that curb or reduce the impact of the present unpredictable conditions (Wingfield 1994).

Studying the response of individual birds to different environmental conditions in the context of seasonal migration has been difficult for logistic reasons. However, a number of species undergo cycles of body mass and behaviour comparable to those observed in free-living species, even under captive conditions (e.g., Berthold 1984, 1996, Gwinner 1986, 1990, 1996, Boswell et al. 1993, Piersma et al. 1995, 1996). Such cycles provide opportunities for studying the intricacies of migratory cycles. We utilized a well-studied captive situation involving two subspecies of a long-distance migrant shorebird species, the Red Knot (Piersma et al. 1995, 1996), to examine the function of corticosterone in the context of the migration-driven annual cycles shown by this species. Food was available continuously and in unlimited supply, thus we assumed that the energy budget was always balanced. The cage-environment, however, diverged from free-living conditions. Do birds perceive an incongruity between observed (captive) conditions and expected (free-living) conditions, and is this manifested as a temporary physiological response, i.e. an elevation of plasma corticosterone concentrations?

Methods

Six Red Knots of the *islandica*-subspecies were captured with mistnets on 15 October 1988 on the intertidal flats south of Schiermonnikoog (53°29′N, 06°12′E), an island in the Dutch Wadden Sea. *Islandica*-knots breed on high arctic tundra in northern Greenland and northeastern Canada, spending the nonbreeding season (August through April) in the large estuaries of western Europe (Davidson and Wilson 1992). All birds were adult, i.e. older than two years. At the Zoological Laboratory in Haren, The Netherlands (53°11′N, 06°36′E) they were kept in an outdoor aviary measuring 2 by 4 m and with a height of about 2 m. At least during the nonbreeding seasons, these knots encountered photoperiods that they would consider normal. The aviary contained a shallow basin with continuously flowing fresh water. The sand and accumulated faeces on the floor were removed every week and replaced with clean sand.

For comparison, six adult Red Knots of the *canutus*-subspecies, breeding in central Siberia and wintering in west Africa (Piersma et al. 1992), were also maintained in captivity. One bird was captured with a clapnet at Iouik on the Banc d'Arguin, Mauritania (19°53′N, 16°17′W) on 1 May 1988 (see Piersma 1988), and the other five were captured with cannon-nets on 18 May 1988 at Eiderstedt Peninsula in Schleswig-Holstein, Germany (54°25′N, 08°48′E) (see Prokosch 1988). Three of the five birds from Germany died for unknown reasons during the last few months of the experiment.

Both captive flocks were fed *ad libitum* with protein-rich (45% of wet mass) trout food pellets (Trouvit, Produits Trouw, Vervins, France). According to the manufacturer (pers. comm.), the pellets were without added hormones. During the weekly cleaning operations the birds were weighed and their plumage and moult scored. Plumage was scored from 1 = grey winter plumage, 2 = trace of the rufous-red breeding plumage, 3 = 1/4 breeding, 4 = 1/2 breeding, to 7 = full rufous-red breeding plumage; the moult of the primary flight feathers was scored in quarters as 0 = old, 1 = in pin, 2 = quarter grown, to 5 = fully grown (Ginn and Melville 1983).

Every four to six weeks we collected blood samples from the 12 birds. After capture in the aviary, we bled the birds from the wing vein into a heparinized syringe as quickly as possible, collecting 1–2 ml of blood. It took 5–38 min from entry into the aviaries to collection of a blood sample. Samples were held on water-ice for 1–3 h until plasma was separated by centrifugation. Plasma samples were stored at −30°C until they were transported frozen from Haren to Seattle, U.S.A.

In Seattle the samples were thawed and 20 μl subsamples of plasma were aliquoted into glass centrifuge tubes to which 300 μl distilled water were added. A total of 2000 cpm (^{3}H)-corticosterone (New England Nuclear) was placed in each sample and allowed to equilibrate overnight at 4°C. The lipid fraction in each sample was extracted with 4 ml of distilled dichloromethane. The organic phase was collected and dried under nitrogen gas at 40°C. The dried extracts were resuspended in 550 μl phosphate-buffered saline with 0.1% gelatin. Aliquots of 200 μl were placed in duplicate assay tubes to be run through the radioimmunosassay. The remaining 100 μl

98

were pipetted into a glass vial to which 4.5 ml scintillation fluid was added (Ultima Gold, Packard Instruments). CPM from each vial were corrected for dilution and provided an estimate of percent recovery of steroid following extraction for each sample. Concentration of corticosterone was determined by specific radioimmunoassay (RIA) according to the procedures described by Wingfield and Farner (1975) but with the modification of Ball and Wingfield (1987). Values of each sample were determined from a standard curve that ranged from 7.8 to 1000 pg and each sample was adjusted for percentage of recovery. All samples were measured in three separate assays. The largest set of samples was collected in 1989. These samples were divided and one portion was run in each of the three assays while those of 1988 were run in the first and 1990 in the last assay. Inter-assay variation based on the standard run in each of the 3 assays was 6.3% (Coefficient of Variation). Recovery values for the three assays ranged from 61 to 100%. Measurements of least apparent steroid were 8.65 ± 0.85 (mean ng/ml $\pm$ SE) and range of percent binding was 90–99% in ligand-free samples. Final concentrations were calculated in units of nanograms per ml of plasma.

The well known increase in corticosterone concentration immediately after capture (the so-called stress-response; see Schwabl et al. 1991, Wingfield 1992, Wingfield et al. 1992, and Wingfield et al. 1995 for discussions), was dealt with in a statistical manner by entering the time elapsed between aviary-entry and bleeding as a covariate in analyses of covariance. We thus assume a linear increase in corticosterone with time since capture over the holding period of up to 38 min. We checked for normality of the data points for corticosterone concentration before doing the statistics. As is illustrated by the central position of the averages within the ranges in Figs. 1C and 2C, this was not a problem.

Results

The six *islandica*-knots examined maintained clear-cut seasonal cycles in body mass (Fig. 1A), wing moult and plumage (Fig. 1B). They showed a mass peak in mid-winter and an even higher mass peak in May–early June, the latter coinciding with the natural period of migration towards the Arctic breeding grounds. In the wild, Red Knots show two, rather than one, body mass peaks before arriving on the breeding grounds in early June (Davidson and Wilson 1992). The first reflects the fuel storage before the migratory flight to one of the two intermediate staging sites (Iceland or northern Norway), the second reflects fuel storage for the subsequent flight to the Arctic. Like their free-living conspecifics, the captive *islandica*-knots moulted from a winter- into a breeding-plumage just before starting to increase in mass in spring. Perfectly in schedule with

wild *islandica*-knots (Piersma and Davidson 1992), a reverse contour feather moult towards a winter plumage took place in August, along with the complete wing moult that lasted into October. The cycles shown by these and other experimental individual Red Knots were maintained for several years (Piersma et al. 1995).

Even though the range of measured and unadjusted corticosterone concentrations was great, values re-
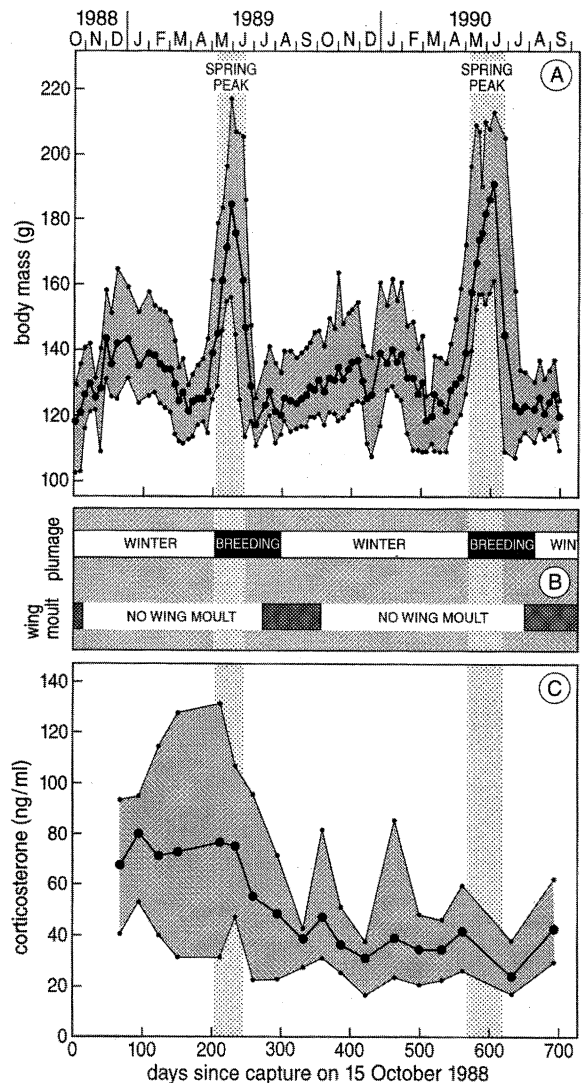

Fig. 1. Long-term variation in body mass (A), plumage type and wing moult (B) and plasma-corticosterone concentration (C) in six *islandica*-knots maintained in captivity for over two years. For the clarity of presentation, not all data points for all individuals are shown. Instead, in panels A and C the averages are shown; the shaded area indicates the range of values since it encloses the minima and maxima. In panel B the periods that the captive Red Knots show a winter or a breeding plumage, and the periods that they are actively growing their primaries are shown. The moulting rhythms of the birds were very synchronous, all six of them starting or stopping body or wing moult within periods of three weeks. The periods covering spring migration (as suggested by mass peaks) are indicated by the vertical bars extending over the three panels.

99

Table 1. Analysis of variance table of plasma-corticosterone concentration in six long-term captive *islandica*-knots. In this model, that explained 53% of the variance in the dependent variable (corticosterone), Bird identity and Phase (spring migration or not) are category variables; "Cage entry-bleeding interval" (min) and "Days after entering captivity" are covariates.

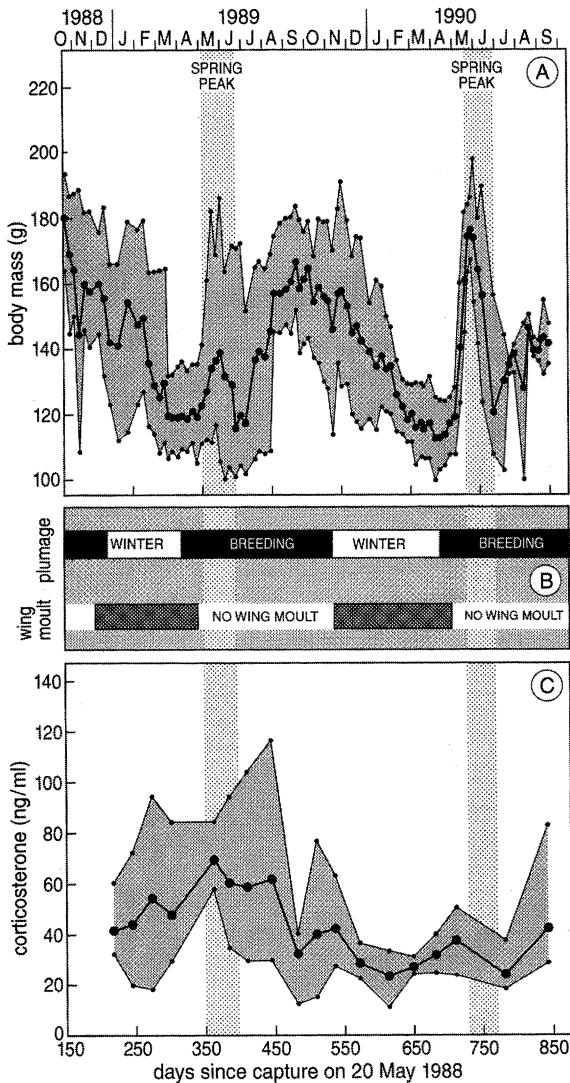| Independent variables	df	Sum of squares	F-ratio	P-value
Bird identity	5	7340	4.045	0.002
Phase of annual cycle	1	2566	7.070	0.009
Bird × Phase	5	4219	2.325	0.049
Cage entry-bleeding interval	1	1048	2.887	0.093
Days after entering captivity	1	16364	45.087	<0.001
Error	90	32666		

Fig. 2. Long-term variation in body mass (A), plumage type and wing moult (B) and plasma-corticosterone concentration (C) over two years in six *canutus*-knots maintained in captivity for almost three years. Graphical conventions as in Fig. 1. Note that the moulting rhythms of *canutus* are not as synchronous as those of *islandica* (Fig. 1), and for this reason the periods of wing moult are rather longer.

mained well within those measured in free-living shore-birds (O'Reilly and Wingfield 1995, Ramenofsky et al. 1995). Corticosterone concentrations showed a continual decrease from the first measurement, 70 days after capture in the wild, to the last measurement two years later (Fig. 1C). There is some suggestion that corticosterone levelled off at 40 ng/ml after about a year, but note that the lowest values were obtained on the penultimate sampling date. An analysis of covariance (Table 1) showed that there were systematic differences in adjusted plasma corticosterone concentrations between individuals, and also that during the spring mass peak, corticosterone reached significantly higher concentrations than during the rest of the year (an increase of about 10%). The magnitude of this effect differed from individual to individual since the interaction between "Bird identity" (individual) and "Phase of annual cycle" (spring migration or not) was significantly different from zero at the 5% level (Table 1). Entering body mass (as a covariate) in the covariance model showed a similar effect (it explained part of the variance in corticosterone, but not significantly so) and obliterated the effect of "Phase of annual cycle". The stress response almost disappeared in the statistical "noise" of the data: there was an increase in plasma corticosterone with the time between the birds starting to be chased in the cage and bleeding, but it was only at a significance level of 0.09. By far the strongest effect on plasma corticosterone concentrations was given by the number of days spent in captivity. This covariate explained as much of the variance in plasma corticosterone as all the previous factors together.

Unlike *islandica*-knots, the seasonal changes of body mass and moult of captive *canutus*-knots did not exactly mirror the patterns of free-living birds (Fig. 2A,B, and see Piersma et al. 1996: Fig. 1). The captive *canutus*-knots showed a spring peak in body mass but then diverged from the normal pattern by having an extended period of elevated mass before loosing weight and going into a contour feather and wing moult later in winter (Fig. 2A,B). Yet, these deviating cycles were maintained over several years in outdoor conditions, and even for a period of two years in a constant indoor

100

Table 2. Analysis of variance table of plasma-corticosterone concentration in six long-term captive *canutus*-knots. In this model, that explained 32% of the variance in the dependent variable (corticosterone), Bird identity and Phase (spring migration or not) are category variables; "Cage entry-bleeding interval" (min) and "Days after entering captivity" are covariates.

Independent variables	df	Sum of squares	F-ratio	P-value
Bird identity	5	1261	0.607	0.695
Phase of annual cycle	1	2674	6.432	0.013
Bird × Phase	5	880	0.423	0.831
Cage entry-bleeding interval	1	2262	5.442	0.022
Days after entering captivity	1	897	2.158	0.146
Error	77	32004		

environment (constant temperature, constant photoperiod, see Cadée et al. 1996). Nevertheless, the results for this group were quite consistent with those for the *islandica*-knots (Table 2). Although there were no significant systematic differences between individual birds, plasma concentrations were elevated (on average by about 20%) during the spring migration mass peak as well. The stress response was more evident than in *islandica*-knots. Although there was a decrease in corticosterone concentrations with time spent in captivity (Fig. 2C), this effect did not reach significance. Overall, corticosterone concentrations were quite similar in both groups of Red Knots, the unadjusted overall means of *islandica* and *canutus* being 51.2 and 44.4 ng/ml, respectively.

Four of the six *islandica*-, and three of the six *canutus*-knots were eventually sexed by post-mortem dissection, and only one of each group appeared to be female. These two females showed temporal patterns in corticosterone concentrations that were identical to the ones of birds identified as males. Hence, we have no evidence for any sex-related differences.

Discussion

In both subspecies plasma concentrations of corticosterone were higher during the northward (or spring) migration than during the southward (or autumn) migratory period. Similar disparities in corticosterone concentrations between the two phases of migration have been observed in other migrants, namely the Western Sandpiper *Calidris mauri* (O'Reilly and Wingfield 1995) and the White-crowned Sparrow *Zonotrichia leucophrys gambelii* (Romero et al. 1997). Overall, however, there was little correlation between body mass, moult cycle and seasonal variation in corticosterone concentration. The outstanding effect, at least for the group of *islandica*-knots, was the long-term decrease in corticosterone with time in captivity. The *islandica*-knots showed natural seasonal mass and moult cycles (Fig. 1; Piersma et al. 1996), and both groups maintained clear-cut annual cycles in several plasma metabolites and thyroid hormones (S. Jenni-Eiermann, L. Jenni and T. Piersma, pers. obs.).

The year-long decline in corticosterone concentrations could be indicative of a long-term adjustment to the stress of capture and handling, or suggest a prolonged effect of the captive environment on an endocrine signal for stress and facultative behaviour. Regarding the former interpretation, we never experienced a change in the degree of escape behaviour upon capture in the aviaries or the ease of handling after capture, even in birds that were held in captivity for over four years. Neither did we find evidence for an interactive statistical effect of bleeding interval and overall time in captivity on corticosterone concentrations.

With regard to the latter interpretation, we note that the movements of captive Red Knots are constrained, and that they do not have to work for their food which consists of pellets rather than buried molluscs. Under such feeding conditions, we assumed little change in the energy balance of the birds throughout the tenure of the study. Although captive birds continue to probe in the layer of sediment within the aviaries, captive conditions are visually (Fig. 3), behaviourally and physiologically rather different from the conditions experienced by birds in the wild. Long-distance migrant bird species such as Red Knots normally encounter a wide range of environments (in terms of climatic conditions, food types, feeding areas and predator densities) in the course of their annual cycle (Piersma 1994). In spite of the fact that environmental conditions in captivity appear congenial (as food is abundant and always available), the steady decline in corticosterone concentrations during at least a year nevertheless suggests that physiological adjustment to such an alien environment takes very long. Thus, we interpret the long-term decrease in corticosterone as mediating appropriate physiological responses of birds normally faced with ecological variability in their environment and the occurrence of unpredictable events. We hypothesize that only after experiencing a full annual cycle in captivity (representing a full sequence of sensitive periods with respect to environmental conditions) do long-distance migrant birds such as Red Knots recognize captive conditions as normal and predictable.

Various studies on passerine birds have suggested that specific qualities or aspects of the habitat are
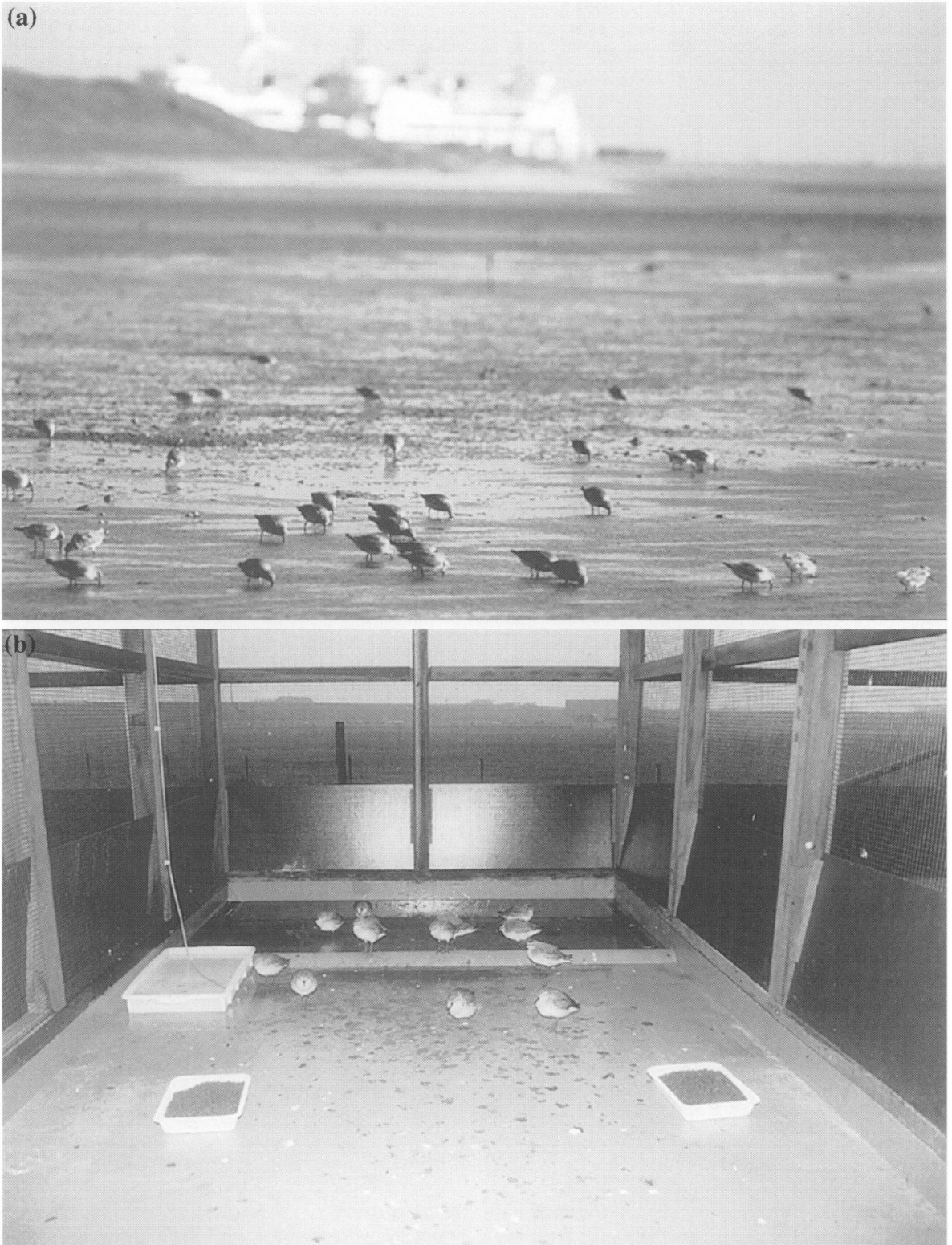
Fig. 3. Photographic documentation of the difference in the environment experienced by free-living (a) and captive Red Knots (b). (a) shows a foraging flock of Red Knots in the western Wadden Sea (Texel, photograph by J. van de Kam). (b) shows birds on the ground in their cage; note the two pellet-containers and the shallow freshwater basin at left (photograph by B. Aggenbach).

critical for successful breeding (Klopfer 1963, Immelmann 1975, Baptista and Petrinovich 1986). Birds learn these specifics during the sensitive period of development. For example, hand-reared White-crowned Sparrows will breed in captivity as the captive conditions are the only experience the birds have known throughout their lifetime (Baptista and Petrinovich 1986). Wild caught White-crowned Sparrows, however, do not complete breeding activities as the captive conditions fail to match those upon which the birds have imprinted during the sensitive phase. If birds are able to identify and imprint on breeding habitats, is it not possible that they may as well recognize localities experienced at other times during the life cycle, such as stop-over sites during migration, or wintering areas? As these habitats are critical for feeding and resting as well as influencing successful completion of the migratory journey, it is reasonable to assume that recognition of conditions or habitats at such localities could be occurring.

Learning or matching expected conditions or stressors to the immediate situation has been linked to a response by the neuroendocrine system involving corticosterone that, in turn, influences an immune response in mammals (Ader and Cohen 1991, 1993). The corticosterone link can be followed further in a study on captive Red Crossbills *Loxia curvirostra* (Hahn et al. 1995). Birds held in captivity showed elevated levels of plasma corticosterone coincident with the pattern observed in free-living birds during the phase of wandering migration. In that study, birds either received, or did not receive the preferred food (hemlock cones) that they expected to locate during that time of the year. Finding the preferred food source (cones) was expected to lead to a cessation of wandering, lowering of plasma corticosterone and initiation of breeding. Contrary to expectation, plasma corticosterone rose further in both groups. This elevation of corticosterone may represent a response similar to the one in Red Knots, as birds adjust or reconcile conditions of captivity with learned or expected natural conditions. Corroboration of our hypothesis in other species held in modified habitats could open up experimental ways to ascertain how free-living birds evaluate the quality and predictability of their environments.

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