Short communication

A relationship between prey density and territory size in non-breeding Eastern Curlews *Numenius madagascariensis*

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Two hypotheses have been proposed to explain the variation in territory size observed within populations. Hypothesis I assumes that individuals can assess the local food density; territory size is then determined by the amount of food contained within the territory (Norman & Jones 1984, McFarland 1986). Under Hypothesis II, an animal defends as large an area as possible and the size of the territory is regulated by intruder pressure from the other animals in the population (Myers *et al.* 1979, Norton *et al.* 1982). These hypotheses need not be mutually exclusive. When territories are used only for foraging, as in non-breeding shorebirds, areas with greater prey densities, providing higher intake rates, are likely to attract more competitors (Goss-Custard *et al.* 1984). These areas therefore will be more costly to defend (Myers *et al.* 1979). Thus, both hypotheses predict a decrease in territory size with increasing food density (Hixon 1980). To distinguish which of these factors proximally controls territory size under field conditions, where manipulations may be impossible, both need to be measured simultaneously (Myers *et al.* 1979, Tripp & Collazo 1997). If the pressure from intruders is partially responsible for regulating territory size, a trade-off in time allocation between foraging and defence should exist (Ydenberg & Krebs 1987). This implies that, to make defence viable, intruder pressure should be related positively to intake rate and negatively to territory size (Carpenter 1987). If no clear relationship between territory size/intake rate and intruder pressure exists, it suggests that the cost of defence is not related to territory size and that the density of the food resource is the major operational force in the system (Hixon *et al.* 1983).

We investigated the relationships between territory size, prey density and intruder pressure in the Eastern Curlew *Numenius madagascariensis* foraging on the callianassid

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shrimp *Trypaea australiensis* during the non-breeding season. This study differed from previous non-breeding shorebird territoriality studies in that the intake rate achieved by birds maintaining territories of different sizes was estimated to establish whether it co-varied with the intruder pressure and density of prey within a territory.

METHODS

Study area and species

The study was carried out in February 2001, on North Stradbroke Island, Moreton Bay, Australia (27°25′S, 153°25′E), on a 2340 × 400-m intertidal stretch a month before the northward migration of Eastern Curlews. All territorial Eastern Curlews (*n* = 35) in the area were undergoing prenuptial moult and were presumed to be adults (2+ years old). Each individual occupied a strip of unvegetated sandflat between mangroves up-shore and seagrass beds down-shore. Thus, individual territories were exposed for about the same duration per low tide.

In this study it was critical to know that the resource being quantified was the one defended by the bird. Three lines of evidence suggest that Eastern Curlews defend reserves of *Trypaea australiensis*: (a) Curlews invariably increase consumption of *Trypaea* during premigratory preparations, when the crustacean accounts for up to 47% of the diet (Y. Zharikov unpubl. data); (b) on a regional scale, Eastern Curlews occur in their greatest densities in the same type of sandy intertidal habitats (Finn *et al.* 2001) as are typically inhabited by *Trypaea* (Hailstone & Stephenson 1961); (c) the only other major prey of the birds, the mictyrid crab *Mictyris longicarpus*, is abundant and mobile (Cameron 1966) and the Curlews do not aggregate in areas with high *Mictyris* abundance (Rohweder & Baverstock 1996). As other prey provide only a small fraction of the diet (Zharikov & Skilleter 2003) they cannot provide a basis for territorial defence (Carpenter 1987).

Territory size

Although birds were not individually marked in this study, most Curlews were easy to identify from peculiarities in behaviour or plumage. Therefore, it was assumed that individuals/territories sampled in this study were independent.

Territory size for each Curlew was estimated as the area (ha) of a rectangle. One side of the rectangle equalled the width (m) of the unvegetated zone between the edges of mangrove pneumatophores up-shore and contiguous *Zostera*-seagrass down-shore. The other side was the sum of half-distances between the centre of the focal territory and centres of the adjacent territories to the right and left. A territory 'centre' was defined as a patch in which the focal individual repeatedly stopped to rest. Once the general area was noted using local landmarks, on the ground such a patch was easy to locate by the presence of numerous

overlapping footprints and faeces. Boundaries between adjacent territories could also be defined because Curlews 'patrolled' them during territorial encounters.

Prey density

Trypaea is a burrow-dwelling callianassid, ≤ 80 mm long. Two measures of *Trypaea* density were taken. (1) For each territory, mean (± sd) density of *Trypaea* burrow entrances per m^2 was estimated by counting them in a 0.3×0.3-m quadrat systematically placed on the surface ten times at 10–15-m intervals between the mangroves and the seagrass edge ($n = 270$). (2) When a Curlew took a *Trypaea* during focal observations, *Trypaea* biomass density (g DM/m^2; where DM is dry mass) was determined exactly where hunting had occurred ($n = 12$). The specific patch of a sandflat was identified by noting a landmark. This was facilitated by the long-shore dimensions of Curlew territories being under 75 m. However, to minimize errors, this was done only when a Curlew continually hunted *Trypaea* for ≥ 90 s. At such a patch, a 2×2-m quadrat was marked within 1 day of the observation. All *Trypaea* present in the quadrat were removed by passing the sediment through a 2×2-mm screen using a manual suction pump. Dry mass (g) of *Trypaea* was determined in the laboratory using an equation relating the large dactyl length (mm) and dry mass ($\log_e[DM] = 2.38 \times \log_e[Dactyl] - 5.83$, $n = 118$, $R^2 = 0.88$, $P < 0.001$, Y. Zharikov unpubl. data).

Intake rates

As some Eastern Curlews also foraged for *Mictyris* crabs, *Trypaea*-intake rates could be determined only for a subset of the observed individuals. The length of a foraging bout, 50.9 min (sd = ±19.8, $n = 24$), was defined by the periodic regurgitation of a pellet of indigestible crustacean matter. One bout was obtained per individual. Continuous observations commenced once the focal individual ejected a pellet, or arrived on the feeding ground from a high-tide roost, and terminated as soon as a (new) pellet was produced. Collected pellets contained recognizable body parts (gastric mill ossicles) of 92% of prey items consumed since previous regurgitation. The length of these ossicles was converted to individual dry mass of consumed *Trypaea* (Zharikov & Skilleter 2003). The sum of individual dry mass values (corrected for the missing 8%) divided by the time spent *Trypaea*-hunting within a bout provided an estimate of *Trypaea*-intake rate.

Time budget

Curlews were observed from 40–100 m using a 20–40× telescope. The following activities were distinguished: (i) foraging, which was subdivided into periods of *Trypaea*-hunting and when other prey were taken; (ii) inactivity; (iii) territorial behaviour; (iv) vigilance. Here, only the time spent hunting *Trypaea* and in territorial encounters is considered relevant to the stated hypotheses. Two indices of territorial behaviour were calculated for each bout: the frequency of territorial encounters (per min) and the proportion of time spent engaged in territorial encounters.

RESULTS

Territory size and territorial behaviour

Eastern Curlew territories measured 0.22–0.87 ha (0.51 ± 0.20 sd, $n = 27$). Territory size was significantly negatively correlated with the density of *Trypaea* holes ($y = -0.0013x + 0.82$, $R^2 = 0.29$, $P < 0.005$) or the biomass (Fig. 1).

Curlew territorial behaviour was highly ritualized and could be assigned to four categories, 'parallel walk', 'upright posturing', fight and chase, that have been well described for other *Numenius* species (Cramp & Simmons 1983). As only two non-territorial Curlews were present in the area, most interactions occurred among the 35 residents. Neither the proportion of time spent in territorial encounters (5.6% ± 6.9 sd, $n = 24$) nor their frequency [0.21 encounters/min (sd = ±0.16), $n = 23$] was related to the territory size. As prey (biomass) density was the only variable explaining variation in territory size significantly, partial correlation analysis was not used.

Functional response

Intake rate increased linearly with *Trypaea* biomass density (Fig. 1). A logarithmic function applied to the same data provided a poorer fit ($R^2 = 0.46$, $P < 0.01$). This is because only two data points were available at high *Trypaea* densities. The distribution of these points suggests that the intake rate may level off at *Trypaea* biomass densities of 4 g DM/m^2 and higher. Neither the frequency of territorial encounters nor the proportion of time spent on territorial behaviour was related to the intake rate.
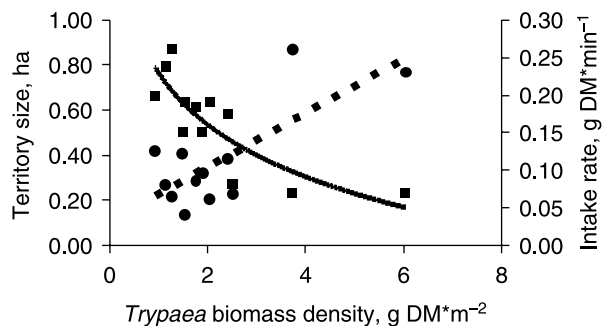

Figure 1. Relationships between the biomass density of *Trypaea australiensis* and territory size (solid line, $y = -0.33 \ln(x) + 0.77$, $R^2 = 0.69$, $P < 0.001$) and intake rate (dashed line, $y = 0.036x + 0.032$, $R^2 = 0.58$, $P < 0.001$) in Eastern Curlews.

DISCUSSION

Finn *et al.* (2001) established that Eastern Curlews in Moreton Bay occurred in greater densities on the substrates occupied by *Trypaea*, which is an important component of this shorebird's diet (Zharikov & Skilleter 2003). This study has demonstrated that the Curlews' territory size and intake rate are strongly correlated with *Trypaea* density. The proportion of time spent on territorial behaviour and the frequency of encounters were unrelated to territory size or intake rate. Although correlative, these results are consistent with Hypothesis I, that in this population territory size is governed by the density of available prey, i.e. the birds have the capacity to assess the density (and amount) of food within their territories. This outcome is similar to the field findings of Hixon *et al.* (1983), McFarland (1986) and Temeles (1987) but apparently contrasts with three previous non-breeding shorebird territoriality studies. Myers *et al.* (1979), Turpie (1995) and Tripp and Collazo (1997) reported that in the Sanderling *Calidris alba*, Grey Plover *Pluvialis squatarola* and Semipalmated Sandpipers *C. pusilla*, respectively, territory size was regulated by intraspecific intruder pressure.

Using modelling, McNair (1987) concluded that territory size should be controlled by whichever factor in the system fluctuates least. Switzer *et al.* (2001) showed that a large population of non-territorial individuals would exert a constant and high intruder pressure on territory holders. As argued by Myers *et al.* (1979) and Tripp and Collazo (1997), large nomadic populations were the reason why intruder pressure controlled territory size in their systems. Similarly, in Turpie's (1995) study, the number of individuals in the study area increased seasonally, increasing intruder pressure on the territorial birds and providing a proximal control for territory size.

An attempt to deplete *Trypaea* stocks experimentally on a Moreton Bay sandflat demonstrated that prey density in the Eastern Curlew – *Trypaea australiensis* system is temporally highly stable (Y. Zharikov unpubl. data). Thus, predictability of *Trypaea* supply to these birds and the rate of intake achieved foraging on this prey are probably high. At the same time, only two non-territorial Curlews were present in our system. Therefore, territorial interactions occurred mostly between resident neighbours. As in other *Numenius* curlews, Eastern Curlews appear generally to be long-lived and demonstrate high within- and between-season non-breeding site fidelity (Marks & Redmond 1996, Finn *et al.* 2002, our pers. obs.). A long site tenancy may lead to memorization of food distribution within a territory and gradual diminishing of 'defence costs over time' (Carpenter 1987, Switzer *et al.* 2001) as familiarity and/ or social hierarchy within the population develop (Davies 1992, Ens *et al.* 1995). A stable hierarchy was found, for example, in non-breeding Eurasian Oystercatchers *Haematopus ostralegus* (Caldow & Goss-Custard 1996), where higher ranking individuals occupy smaller habitat patches providing predictably higher intake rates year after year (Ens & Goss-Custard 1986). Younger birds either did not defend territories or had to use areas with considerably lower resource densities (Goss-Custard *et al.* 1984). Because our study captured only the end of a 6-month non-breeding season, it is likely that the birds had already solved any problem they originally faced of securing a territory. So the intensity of interactions could be important in determining territory size when the territories were established (or re-established) at the start of a season, but it was no longer a factor at a season's end, when a social hierarchy may have been formed and the higher-ranking birds seized the patches yielding higher intake rates. Indeed, in 1998–2000 and 2000/01 the proportion of time spent on territory defence decreased through the non-breeding season (6.0–4.0% and 7.3–5.6%, respectively, Y. Zharikov unpubl. data). The pattern is similar to other non-breeding territorial shorebird (Johnson *et al.* 1981, Turpie 1995) and non-shorebird species (Gwinner *et al.* 1994) and probably represented a genuine decrease in the intensity of agonistic interactions. It is worth noting that the two Curlews observed in the study that failed to secure a territory were subadults (< 2 years old). If our results apply to the broader scale (e.g. Finn *et al.* 2001, 2002), one prediction would be that *Trypaea*-sandflats are mostly occupied by adult Curlews whereas the inferior (muddy) intertidal areas elsewhere in the bay, where lower intake rates may be achieved, may contain a sizeable proportion of subadults. Considering that 27% of the Eastern Curlew population oversummer rather than migrate to breed (Finn *et al.* 2002), acquisition of a high-quality non-breeding site in this population may be a prerequisite for successful migration and subsequent nesting (cf. Ens *et al.* 1995, Ekman *et al.* 2001).

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