The ontogeny of home ranges: evidence from coral reef fishes

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The concept of home ranges is fundamental to ecology. Numerous studies have quantified how home ranges scale with body size across taxa. However, these relationships are not always applicable intraspecifically. Here, we describe how the home range of an important group of reef fish, the parrotfishes, scales with body mass. With masses spanning five orders of magnitude, from the early postsettlement stage through to adulthood, we find no evidence of a response to predation risk, dietary shifts or sex change on home range expansion rates. Instead, we document a distinct ontogenetic shift in home range expansion with sexual maturity. Juvenile parrotfishes displayed rapid home range growth until reaching approximately 100–150 mm length. Thereafter, the relationship between home range and mass broke down. This shift reflected changes in colour patterns, social status and reproductive behaviour associated with the transition to adult stages. While there is a clear relationship between body mass and home ranges among adult individuals of different species, it does not appear to be applicable to size changes within species. Ontogenetic changes in parrotfishes do not follow expected mass–area scaling relationships.

1. Introduction

Animal movement patterns are dynamic in space and time, and are a fundamental component of a species’ ecology [1,2]. With the exception of migrations, most movements by animals are restricted to a home range. However, this home range is rarely consistent over time and is likely to change as a result of changing demands and abilities as the animal grows and matures [1,3–5]. Throughout its life, the size of any animal’s home range is driven by three key demands. Animals must shape their home ranges to avoid predation, find adequate food, and then reproduce. As animals grow, their body size changes their vulnerability to predators. In high-diversity systems with a wide array of predators, smaller animals are more vulnerable and, as such, must take steps to minimize predation risk. This can be accomplished by reducing movement or avoiding risky locations, thus restricting an animal’s home range [6–8]. With growth, the range of potential predators reduces, as does overall predation risk, which permits home range expansion [9,10]. Similarly, as animals grow, the nutritional demands of a larger body must be met, often demanding a greater area to procure necessary food [11–13]. Following maturation an animal will need to find a mate and reproduce. Home ranges, therefore, must be large enough to ensure adequate encounters with potential mates [14,15]. While these drivers place seemingly simple demands on an animal’s home range, the responses of animals are complicated by concurrent ontogenetic shifts in physiological and social factors, which can also shape changes in home range size and patterns of use. As such, determining the relative importance of specific drivers in shaping changes in home range sizes can be difficult.

Disentangling the various drivers and responses can be challenging. For example, flight and associated high levels of parental care essentially remove the effects of growth on the home ranges of fledged birds [16]. Similarly, in mammals the effects of parental care and highly complex social systems often lead to highly intertwined effects of home range drivers [17]. However, in...
lower vertebrates these drivers may be more clearly separated. For example, varanid lizards (e.g. Komodo dragons, Varanus komodoensis) provide useful models, as they undergo considerable growth following hatching and their home ranges are less impacted by parental care than mammals’ or birds’ [8,18]. Coral reef fish are another useful model to study the ontogeny of home ranges. Following a brief period in the plankton, postsettlement fish grow by several orders of magnitude on the reef, experiencing temporally separated events including diet shifts, maturation and sex change. This temporal separation enables us to explore the relative impact of predation, diet and reproduction on lower vertebrates using reef fishes as a model.

In addition to understanding the factors affecting the ontogeny of home ranges, it is crucial to understand the ecological consequences. Any shift in an animal’s home range can profoundly impact its interactions with its environment [2,19]; as such, it is important to understand how these factors change over the course of its life [20,21]. Coral reefs in particular are highly reliant upon several functional groups of herbivorous reef fishes to maintain their resistance and resilience to disturbances [22]. Parrotfishes (scarine Labridae), with their unique jaw morphology and numerical abundance, dominate several of these functional groups [23]. Recent research, however, suggests that the ecosystem functions of parrotfishes depend on their home-ranging behaviour [24,25]. While it is well documented that the role of herbivores changes with ontogeny [26–28], it is not yet known (i) how the home range of an individual scales with body size and (ii) which factors are most important in determining changes in home range size through time.

This study examines the ontogeny of home ranges of three parrotfish species from early postsettlement (approx. 10 mm, 0.01 g) to adulthood (over 300 mm and 1 kg). This represents a change in mass of over five orders of magnitude and incorporates a dietary switch, from carnivory to detritivory, maturation and protogynous sex change. During this time, individuals are also subjected to distinct changes in predation risk, social and reproductive demands [9,29], and nutritional needs [29], which may also drive home range shifts. As such, these fishes may provide novel insights into the relative importance of predation, nutrition and reproduction, alongside other social factors, in shaping ontogenetic scaling of home ranges in lower vertebrates.

2. Material and methods

(a) Data collection

Field observations were conducted on Lizard Island, on the mid-shelf of the Great Barrier Reef (14°41’5” S, 145°26’55” E). The primary study site was North Reef, an obliquely exposed fringing reef extending from a distinctive crest (1 m below chart datum) down to the reef base at 8–9 m. Home ranges were estimated for three species of parrotfish (scarine Labridae; [30]), Scarus frenatus, Scarus niger and Chlorurus sordidus. Home ranges were estimated from direct observations, using three slightly differing methods, owing to the wide range of size classes observed. First, for juvenile parrotfishes (20–150 mm total length; TL), a scale map was used. The reef front (approx. 80 m across) was mapped by recording prominent features, which were used as reference points. The distances between reference points were measured, and by triangulation, a two-dimensional scale map of the whole area created. Areas were estimated based on a planar two-dimensional plot (where necessary the plot conformed to any larger three-dimensional surface complexity; landmark features would thus follow the benthos, as a small fish would). The locations of fishes were subsequently recorded in relation to the reference points. Where ranges were very small, additional reference points were used to provide more detailed local maps.

Once a fish was located on the reef, it was identified to species, its size estimated and any distinguishing features noted to allow individual identification (colour markings and parasite scars were particularly useful). Each focal fish was followed for a series of 30 min observation periods, marking its position every 15 s on a localized scale map. These data points were then transferred onto overlays of the main scale map and the area of the home range measured (as a convex polygon) using a digital graphic pad. Individuals were followed for a minimum of four 30 min periods or until the cumulative home range area (based on minimum convex polygons; MCPs) reached an asymptote (i.e. area occupied did not increase by more than 2%). This usually required six to nine periods. No more than two observations were made per day, separated by at least 3 h. Ranges were estimated over a period of no more than 10 days, as they rapidly expanded with fish growth. The cumulative area occupied over the entire observational period was taken as the estimated home range. Owing to low population densities of C. sordidus, data on this species were supplemented by a few (six) individuals from the Lizard Island lagoon using identical methods.

Extremely small or recently settled fishes (less than 25 mm) were observed once, for 30–60 min. The shorter observation times for these smaller size classes were necessary because of difficulties in relocating and re-identifying individuals. Once located, small individuals were observed constantly until they occupied no new areas within a 5 min period. Maps of the substratum and key features were made immediately after observations ceased and triangulated as described above. The observations on small individuals were predominantly in the austral summer, November to February (coinciding with peak recruitment). To allow for the short observation periods, the final estimated home ranges of the smaller fish were scaled up based on a calibration equation derived from cumulative area–observation time relationships obtained for the larger specimens described above (see the electronic supplementary material, equation S1).

Finally, for larger fishes (more than 150 mm; more than 143 g), an aerial photograph of the study site was used to construct a scale map of the area. Once major features were identified (e.g. gutters and outcrops), additional underwater features were added and their position fixed by triangulation, as above. Again, individual fishes were identified based on size, body patterns and (most reliably) abnormalities (scars, parasite deformities, etc.). For S. frenatus and S. niger, most individuals in the area were identified and used; for C. sordidus, only individually recognizable fish were used. The majority of observations were conducted during two three-month periods when the site was visited most days. Ranges were based on a minimum of 5 h of cumulative observations or as a result of 50+ individual sightings. Locations were plotted on the map, and home range areas were again estimated using MCPs.

(b) Statistical analyses

For each individual, body mass was calculated using length–weight regressions [31]. The relationship between fish mass and home range area was initially examined using raw data, the most appropriate model to describe the relationships between body mass and home range being fitted to the entire dataset. The relationship was subsequently assessed separately.

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for juveniles (less than 150 mm) and adults (more than 250 mm). Several regression models (linear, logarithmic, power, growth and exponential) were fitted to the data and the model with the highest $r^2$ value was selected for the overall relationship, then juvenile and adult individuals separately (see electronic supplementary material, table S1). Once the model was selected, the inflection point (i.e. the point in a curve where the slope of the tangent equals 1) and associated errors from the model were calculated using MATLAB.

To provide a dimensionally balanced view of fish size and habitat areas, body mass data were cube-root transformed to provide a shape-independent, one-dimensional metric of increasing body size. Estimated home ranges were then square-root transformed to provide a one-dimensional measure of home range size. The residual data from the model fitted to these transformed data were then used to test for variation among species (as these data had lower variance than untransformed data). Interspecific variability in the home range size to body mass relationship was assessed using a one-way ANOVA. The analysis compared the residual data from the model for each species to determine whether there was a significant difference in the model’s fit between species. The home range size of IP (initial phase) and TP (terminal phase) individuals were compared using a two-sample $t$-test.

3. Results

The home ranges of 75 fish were estimated: 42 *S. frenatus* (15–356 mm TL), 14 *S. niger* (11–304 mm TL) and 19 *C. sordidus* (10–240 mm TL). A logarithmic model was found to provide the best fit for the relationship between body mass and home range size for these three species (home range $= 24.40 \ln[\text{body mass}] + 55.58$; figure 1). This model was significant, with body mass explaining 76% of the variability in the home range data ($r^2 = 0.76$; $F_{1,73} = 236.44$, $p < 0.001$). The inflection point of the curve occurred when body mass equaled $24.4 \pm 1.6$ g. This corresponds to a length of $106.9 \pm 4.4$, $106.9 \pm 4.4$ and $107.0 \pm 4.5$ mm (TL ± error associated with the model) for *S. frenatus*, *S. niger* and *C. sordidus*, respectively (see electronic supplementary material, figure S1). After this point, the rate of increase in home range per unit body mass was significantly reduced. A power curve also provided a good statistical fit, but only for small individuals; it explained little variation in larger specimens (see electronic supplementary material, table S1).

The relationship between the cube root of body mass and the square root of the home range size, a scale-independent relationship between mass and home range area, was also best modelled with a logarithmic regression (home range $^{1/2} = 4.39 \ln[\text{body mass}^{1/3}] + 5.52$; figure 2). The model was significant and explained 87% of the variation in the data ($r^2 = 0.87$; $F_{1,73} = 484.43$, $p < 0.001$). All three species exhibited similar patterns of home range growth with no significant differences in the residuals among species (ANOVA in the electronic supplementary material, table S2). Despite the logarithmic relationship being significant for the overall pattern, two distinct components within the relationship were evident. Juveniles (less than 150 mm) displayed a rapid increase in home range size with growth; home range expansion with body mass was best described by a power curve regression (home range $= 13.40 \times [\text{mass}]^{0.71}$; $r^2 = 0.79$; $F_{1,53} = 201.25$, $p < 0.001$; electronic supplementary material, table S1b). Above a length of 100–150 mm (106.9–107.0 mm based on the calculated inflection points), there was a breakdown in the size–area relationship, with adults displaying no significant relationship between body mass and home range size, and with no significant difference in home range size after changing sex ($t$-test; $t = 0.57$, $p = 0.58$).

4. Discussion

We quantified the home range size of parrotfish species at every postsettlement stage of their development, covering an increase in mass of over five orders of magnitude. This increase in size leads to considerable shifts in predation risk, nutritional demands, maturation and, in some individuals, a protogynous sex change [9,32–35], all of which can potentially drive changes in home range size. Where ontogenetic effects on home ranges have been studied, the causes of the changes have generally proved

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**Figure 1** Relationship between body mass (g) and home range size (m$^2$) for *S. frenatus*, *S. niger* and *C. sordidus*. Triangles represent juvenile individuals, and squares and circles represent initial phase and terminal phase individuals, respectively. Grey triangles indicate juveniles, which are predominantly omnivores/carnivores (following [19,29]). The dotted vertical line indicates the maximum body mass achieved before *S. frenatus* and *S. niger* undergo juvenile to adult colour changes, and *C. sordidus* shifts from solitarily to schooling behaviour.

**Figure 2** Scale-independent relationship between body mass and home range size. To remove the effects of scale, body mass was cube-root transformed and home range areas were square-root transformed. Data are presented for all species; *S. frenatus*, *S. niger* and *C. sordidus*, with the dotted line representing the size at maturity. The fitted line is a logarithmic regression; see text for details.
difficult to disentangle. Examples from birds and mammals are hampered by relatively limited growth and a high degree of parental care [36–38]. Nevertheless, predation, nutritional needs and reproduction have been repeatedly identified as key potential drivers [2,3,8,39]. In reef fishes, the clear separation of growth and associated changes in trophic and sexual status may permit a better understanding of the factors driving ontogeny of home ranges. As a result, we can begin to identify the roles of potential drivers of home range size versus body mass relationships in one group of lower vertebrates, the parrotfishes. In particular, three factors, predation, trophic and reproductive demands, can be addressed separately.

(a) Does predation restrict home ranges?
For small reef fishes, as with all small organisms, the risk of predation is extremely high [32–34]. In such a hazardous environment as coral reef, fishes face a trade-off between foraging and remaining in, or near, shelter [32,40]. Predation pressure is therefore likely to limit movement in small fishes [41]. As they grow, however, larger body size enables home range expansion, probably as a result of increasing handling costs for predators seen in both reef fishes [10] and forest birds, for instance the junco (Junco phaeotus) [42]. Therefore, if predation were the primary mechanism driving the mass–area relationship in parrotfishes, we would expect initially slow expansion of home ranges in juveniles, followed by a rapid increase in the area occupied as fish grew and predation risk declined. This is not the case for juvenile parrotfishes, as they rapidly expand their home range from the smallest size observed. The breakdown in the relationship observed in larger fishes (more than 100–150 mm) may result from a size threshold above which a new suite of predators become important. However, this seems unlikely as reef predators are capable of handling a wide size range of prey, with the vast majority targeting small fishes [10,34]. Overall, home ranges do not expand in a manner consistent with decreasing predation. This suggests that other factors, for example food availability, may be more important.

(b) Trophic constraints on home ranges
Rapid expansions of home range with body size, comparable with those seen in juvenile scarids, are occasionally observed in species seeking food resources when food is limited. This has been seen in many reptile species, including Komodo dragons [8], and some mammalian species, including ground squirrels (Spermophilus beldingi) [1,12,17], all of which forage for widely dispersed, cryptic food resources. Small parrotfishes inhabit the epilithic algal matrix (EAM) following settlement [43], preying on small cryptobenthic crustaceans and other invertebrates [29]. While these invertebrates are highly abundant on coral reefs [44], the rate at which small parrotfishes expand their home ranges suggests that not all invertebrates are available to the fish and that larger ranges are needed to access adequate food resources. The complex three-dimensional structure of the EAM might provide shelter for the prey. This, in conjunction with the limited gapes and jaw strength of juvenile parrotfishes [26] suggests that they are only able to detect and acquire prey close to the surface of the EAM. Thus, a larger home range would be required to increase prey encounter rates. This type of demand has previously been documented in cheetahs [7] and is especially prevalent in taxa with insectivorous life stages, for example tropical lizards [8,45]. Despite insects being highly abundant on land, their availability is patchy. Consequently, terrestrial insectivores require large home ranges to encompass sufficient resources. Parrotfishes follow this pattern throughout their invertevorous stage, suggesting that the distribution of available invertebrate prey might be comparably sparse or patchy.

Larger juveniles continue to exhibit rapid home range expansions with body mass, despite a marked dietary shift from crustaceans to detritus and algae (based on specimens collected from this study location [29]). Juvenile scarids possess small beaks and as such can only make relatively shallow bites [26]. With their limited bite size, juvenile parrotfishes may therefore have to make a disproportionately large number of bites over a large area to ingest sufficient nutrients or to seek out patches of high-quality EAM, with low sediment loads and a high detrital component [46]. Again, large home ranges would increase the chances of encountering sufficient high-quality food.

Overall, it would appear that the relationship between somatic size and the home ranges of juvenile parrotfishes is influenced primarily by the need to acquire high-quality resources rather than directly avoiding predation risk. However, predation pressure may be indirectly involved. By accessing a large quantity of resources of the highest nutritional quality, juveniles are able to grow rapidly, minimizing the time they must spend in life stages that are subjected to the highest rates of predation.

Following maturation, home ranges cease to expand at the same rate. This may, in part, be owing to parrotfish functional morphology. The strength and size of adult parrotfish beaks are significantly greater than those of their juvenile counterparts [47]. This allows them to bite deeper into the EAM, removing greater volumes of algae, invertebrates and particulate organic matter [29,48,49]. By adding a new dimension (depth) to their feeding, it appears that adult parrotfishes can access more resources per area than juveniles, which can only scrape the surface [26]. Similar changes in function are observed in terrestrial and marine reptiles, with potential impacts on their home ranges [8,21,50]. While changing functional capabilities may explain why home range expansion can cease, it does not explain the relatively rapid transition. This appears to be driven by social interactions.

(c) Reproductive constraints on home ranges
Between 100 and 150 mm, the relationship between somatic size and home range changes and parrotfishes exhibit a marked ontogenetic shift in their home-ranging behaviour. Adult fishes had home ranges of between 160 and 300 m², which are broadly comparable to other Pacific and Atlantic parrotfishes [51,52]. If home range expansion continued to follow the pattern seen in the juveniles, an individual would occupy approximately 16 000 m² by the time it reached 300 mm (TL). This is over 50 times larger than any home range found in adults. Why home ranges cease to expand with body size is particularly interesting and raises several questions: how are adults able to acquire sufficient resources to meet metabolic demands, especially given that juveniles respond to their environment as if they are resource
limited, and what mechanism drives the marked change in the relationship?

The social status of parrotfishes directly influences their ecology [51,53,54] and may be responsible for limiting home range expansions in adult fishes [29,55]. The breakdown in the area–mass relationship corresponds closely with reported colour changes in two of the three focal species. These colour changes are associated with the transition from juvenile to initial phase adults, and occur at approximately 120 mm for both S. frenatus and S. niger [42]. Following colour changes, the new initial phase adults of these species join small social groups, or harems, with a single aggressive male defending a fixed territory. This social transition corresponds closely with the changing area–mass relationship observed in our study, where the home ranges of relatively small individuals rapidly increase until they match the size of the harem leader's territory. Thereafter, home ranges no longer increase with an individual's somatic size. This pattern of territorial range delineation has been recorded in a number of other social taxa, such as cheetahs (Acinonyx jubatus; [7]), red deer (Cervus elaphus; [36]) and coyotes (Canis latrans; [56]), in which young individuals occupy the territory of their parents or social group [52,57,58]. This social control of home range expansion after maturity might be the reason why we see no evidence of an effect of the change in sex (and colour) associated with a transition from initial to terminal phase in adult parrotfishes.

Chlorurus sordidus individuals do not exhibit drastic colour changes as they transition from the juvenile to initial phase, and do not form aggressively defended harems. However, at around 90 mm long, juveniles of this species shift from being solitary occupants of sheltered back-reefs or deeper areas, to schooling, mature adults, most frequently occupying shallow, exposed fore-reefs [42]. In parallel with this behavioural shift, the area–mass relationship again changes abruptly, as seen in the harem species. While schooling species have significantly fewer aggressive interactions, they too remain site-attached as adults, apparently occupying areas of familiarity to facilitate escape from predators or aggression from other species [59,60].

Many studies have highlighted the predictability of the mean home range size of a species, given its average body size: a standard interspecific scaling relationship [12,45,61]. Within species, however, marked changes in the rate of home range expansion are often associated with ontogenic changes in diet. Reptiles are among the best examples of this phenomenon, with some species exhibiting wholesale shifts in diet, habitat and home-ranging behaviour as they increase their body mass [8,50]. In the parrotfishes, the cessation of home range expansion, despite continued somatic growth, is markedly different. In parrotfishes, the effect of changing diet or predation risk seems to have little influence on spatial use patterns. Instead, for adult parrotfishes, complex social systems appear to drive their home range–size relationships: a pattern with strong parallels to those relationships seen in social birds and mammals. In birds, mammals and other taxa living in social groups, the size of a social group's territory is often described as a 'minimum economically defensible area', where all members of a social group have access to the group's entire territory [4,62]. In these examples, as in parrotfishes, body size does not play a significant role in determining the home range size of an individual within the group.

This study highlights the need to assess the spatial behaviour of organisms at all stages in their growth and development in order to understand the nature of home-ranging behaviour. With growth, juvenile parrotfishes displayed rapid increases in home range size, which appears to be driven by increased nutritional demands. A distinct change in the rate of home range expansion mirrors changes in colour patterns and appears to be shaped primarily by social factors associated with sexual maturity [42], while changes in body size, diet and sex appear to have a limited impact on the overarching area–size relationship. Overall, juvenile parrotfishes operate similar to forest dwelling lizards, while adults operate similar to social mammals. Our observations suggest that for fishes, inter- and intra-specific size–area relationships may be shaped by markedly different drivers.

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