Evolutionary Ecology Research, 2013, **15**: 103–110

Intraspecific home range scaling: a case study from the owl limpet (*Lottia gigantea*)

Phillip B. Fenberg

Department of Zoology, Oregon State University, Corvallis, Oregon, USA

ABSTRACT

Background: The owl limpet (*Lottia gigantea*) is an ectothermic invertebrate that inhabits the rocky intertidal zone where it territorially defends home ranges and grazes algae growing on the rocks. Among endothermic species, home range scales isometrically with body mass.

Hypothesis: Home range area scales isometrically (scaling exponent ~1.0) across individuals of the owl limpet, spanning more than an order of magnitude in body mass.

Field sites: Southern and central California rocky intertidal sites ($n = 5$; ~32.5–35.5°N).

Methods: Measure home range area and body mass of individuals ($n = 104$). Determine the scaling exponent.

Conclusions: Home range scaling across individuals of *L. gigantea* exhibits the same isometric relationship that is often found across endothermic species.

Keywords: Allometry, ectothermic invertebrate, home range scaling, *Lottia gigantea*, size-selective harvesting.

INTRODUCTION

Body size correlates with many different facets of the ecology and life history of a species and is generally considered to be one of the most important traits of an organism (Calder, 1984; Anderson-Teixeira *et al.*, 2009; Sibly *et al.*, 2012). The observed generality of some body size scaling relationships has profound implications for describing ecological organization, from species to ecosystems (Brown *et al.*, 2004; Woodward *et al.*, 2005; Hendriks, 2007). For example, the scaling of home range area with body mass is often observed to be isometric (power function exponent ~1.0) when measured across endothermic species spanning multiple orders of magnitude in size (Lindstedt *et al.*, 1986; Jetz *et al.*, 2004; Makarieva *et al.*, 2005; Marquet *et al.*, 2005):

$$Hr = Y_o M^{\sim 1}$$

where Hr is home range area, Y_o is a normalization constant, and M is body mass.

Correspondence: P.B. Fenberg, Department of Zoology, Oregon State University, 3029 Cordley Hall, Corvallis, OR 97331, USA. E-mail: pfenberg@gmail.com; fenbergp@science.oregonstate.com
Present address: University of Colorado, Museum of Natural History, Boulder, CO 80309, USA.

The home range scaling relationship has been an important component for explaining patterns of space use and resource partitioning in ecology (Jetz *et al.*, 2004; Marquet *et al.*, 2005). Yet with all the advances made over the past few decades in measuring and applying this scaling relationship and developing theory, nearly all of the research has been focused on between-species patterns, particularly for endothermic species (but see Nilsen and Linnell, 2006). Whether this relationship is also observed across individuals of a single ectothermic species is not known but necessary to uncover the potential generality of home range scaling at multiple levels of ecological organization.

Marine gastropods are ideal study organisms in which to measure intraspecific home range scaling because individuals grow continuously throughout their lives (i.e. indeterminate growers), and home range size may be measured with relative ease in some species, such as rocky intertidal limpets. The owl limpet (*Lottia gigantea*), for example, is a particularly amenable study organism for the reasons mentioned above. *Lottia gigantea* is a large patellid gastropod (Lindberg *et al.*, 1998), capable of attaining lengths in excess of 100 mm. It has a range from southern Baja California (~26.1°N) to northern California (~39.4°N) along the Pacific rocky intertidal coast (Fenberg and Rivadeneira, 2011). Individuals inhabit multiple rock types in the mid to high intertidal zone (Sagarin *et al.*, 2007), where they graze on a thin layer of algae. *Lottia gigantea* is a protandric hermaphrodite, in that individuals start their reproductive lives as males and change sex to become females as they age and grow larger (Fenberg and Roy, 2012). Medium to large individuals (generally females) territorially defend their algal grazing area, while smaller individuals are non-territorial (generally males) and are known to periodically raid territories before being 'bulldozed' away (Stimson, 1970; Schroeder, 2011). However, because an *L. gigantea* territory provides all of the area needed to acquire resources for growth and reproduction (i.e. the home range), the two terms are used interchangeably for this species (Stimson, 1970; Wright, 1989; Schroeder, 2011).

Lottia gigantea is size-selectively harvested throughout much of the central portion of its geographic range (Sagarin *et al.*, 2007; Fenberg and Rivadeneira, 2011), reducing mean and maximum body size of exploited populations, resulting in cascading effects on their ecology and life history (Fenberg and Roy, 2012). However, sex ratios are stable across populations due to reduced size at sex change at harvested sites (Fenberg and Roy, 2012) and Makarieva *et al.* (2005) showed that home range scaling does not generally change with ecosystem disturbance.

In this study, I tested the hypothesis that an isometric scaling relationship between home range area and body mass (commonly observed across endothermic species) is found across individuals of an ectothermic marine invertebrate, *L. gigantea*. Specifically, I tested if the log-log slope of home range area versus body mass is significantly different from 1.0 (i.e. an isometric power function exponent). If a tight correlation with isometric scaling is also found at the intraspecific scale, then hypothesized causal mechanisms may indeed apply generally – encompassing a spectrum of sizes from individuals to wider taxonomic groups. I also tested whether the scaling relationship is different across individuals from exploited and protected sites to determine if harvesting significantly changes the rate at which home range scales with body size.

MATERIALS AND METHODS

Body mass

I collected 173 individuals of *L. gigantea* during the fall and winter months of 2003–2005 when individuals were gravid (Kido and Murray, 2003). The individuals collected ranged in size from 17.8 to 70.1 mm (mean = 37.4 mm; S.E. = 0.84 mm). The mass of each individual (weight including the shell, minus epibionts, paper towel dried) was measured to the nearest gram and plotted against shell length (mm). I then fit a power function through the data, revealing a tight correlation ($r^2 = 0.975$; $P < 0.0001$). I used the equation

$$\text{Mass (g)} = 0.00009*\text{Length (mm)}^{3.0471}$$

to extrapolate the mass of all measured individuals described below.

Home range

All field sites sampled are located in the central range of *L. gigantea* (southern and central California; from 32.7 to 35.5°N), which is characterized by high local abundances compared with the peripheral portions of its geographic range (Fenberg and Rivadeneira, 2011). Two sites (Cabrillo National Monument, 32.7°N and Vandenberg Air Force Base, 34.7°N) are characterized as having minimal or no harvesting pressure, while the remaining three sites are characterized as being subjected to some harvesting pressure [Ken Norris Rancho Marino, 35.5°N; Point Fermin, 33.7°N and Cortez Street, 32.8°N (for further site descriptions, see Fenberg and Roy, 2012)]. Protected sites harbour significantly larger individuals and thus provide the upper range of body mass and home range areas for this species (Sagarin *et al.*, 2007; Fenberg and Roy, 2012).

Individual home ranges can often be identified by the distinctive radular marks left in the algal film by the limpet (Fig. 1), which generally resides at the edge of its home range at low tide (Stimson, 1970; Shanks, 2002). Home ranges may also be well defined by the presence of one individual surrounded by an area of unsuitable habitat (e.g. macroalgae, mussels or other mid-intertidal sessile invertebrates). I searched the mid-intertidal zone of each field site for a total of 40 minutes, during which I took high-resolution digital photographs of home ranges and measured the sizes of the occupier. I measured the home range area only for individuals living on flat surfaces due to the difficulty of measuring area for highly rugose surfaces. I measured the area of each home range (mm^2) using image-analysis software (Image J, version 1.34s). In total, I quantified the relationship between home range size and body size by measuring the lengths of 104 individuals (range 30–82 mm) and the areas of their respective home ranges from two protected ($n = 27$) and three exploited sites ($n = 77$). I converted the length of individuals to mass using the equation above.

Sex ratios are stable across exploited and protected populations due to reduced size at sex change in exploited populations (Fenberg and Roy, 2012), thus my measurements should span the biologically realistic size distribution of females (> 30 mm) and their associated home ranges across populations. Thus, most of the individuals measured for the home range analysis were likely female – but there are no secondary sexual characteristics available to distinguish between the sexes, so some of the measured individuals may also have been male (it is possible that some large males occupy territories).

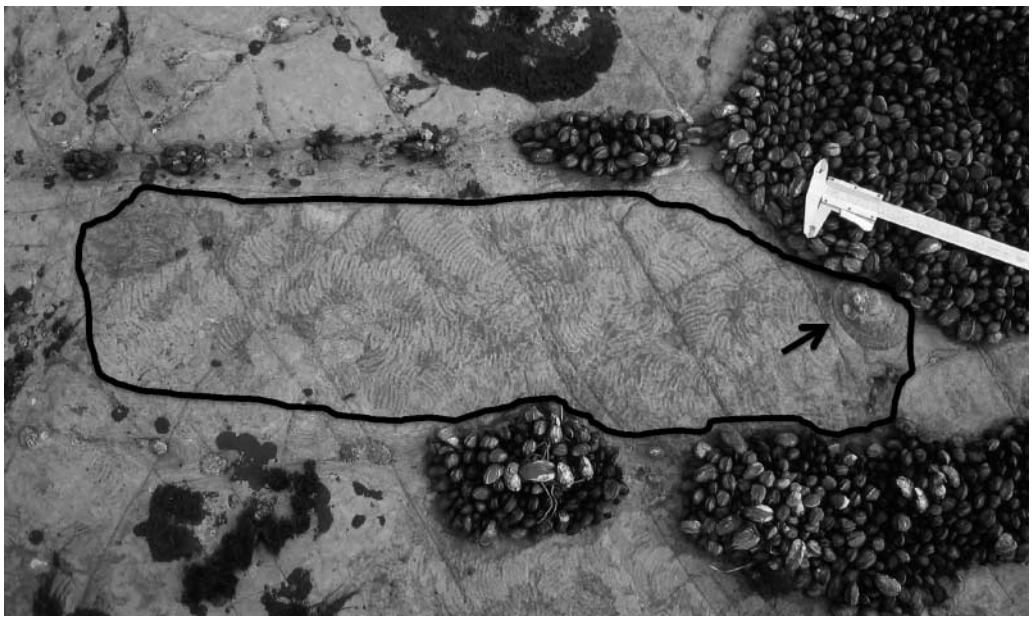

Fig. 1. Picture of a typical *Lottia gigantea* home range. The individual (marked by an arrow) is 82 mm long with a territory area of 185,731 mm^2. Close inspection of the substrate reveals distinctive radula marks that outline the extent of the home range (approximately outlined with a black line).

I employed linear regression for a log-log plot of home range area (mm^2) versus body mass (g) and calculated 95% confidence limits around the slope to determine if 1.0 was included in the estimate. In addition, I tested if the slope was different from 1.0 by changing the null hypothesis on a linear regression model from a slope of 0.0 to a slope of 1.0 for the whole dataset and separately by protected and exploited sites. All analyses were done in R (R Development Core Team, 2012).

RESULTS

The power function equation fit through home range area (mm^2) versus body mass (g) is: $Hr = 2709M^{0.98}$ ($r^2 = 0.76$; $P < 0.0001$), showing an isometric scaling relationship. On the log scale, 95% confidence limits on the slope include the hypothesized prediction of 1.0 (slope = 0.983; 95% CI ± 0.11). In addition, the slope of 0.98 is not significantly different from 1.0 ($P = 0.767$) when changing the null hypothesis on a linear regression model from 0.0 to 1.0. When analyses are done separately by harvesting pressure, the slopes are not significantly different from 1.0 for individuals from exploited sites ($P = 0.265$) and protected sites ($P = 0.09$), justifying pooling individuals from different sites for the overall trend (Fig. 2). These results indicate that home range scaling across *L. gigantea* individuals is isometric.

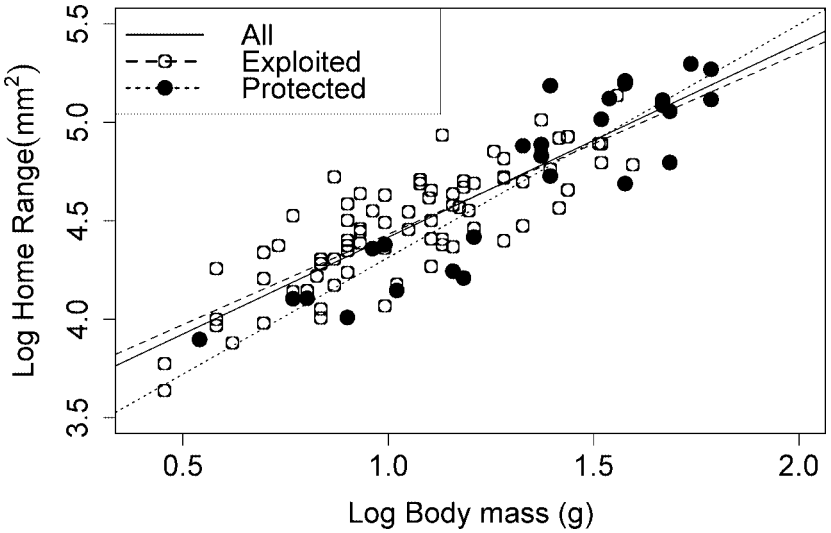

Fig. 2. The log-log relationship between home range size (*Hr*) and body mass (*M*) across 104 *Lottia gigantea* individuals (regression for all individuals: $r^2 = 0.76$; $P < 0.0001$; $\log Hr = 0.98 * \log M + 3.43$). Each data point represents one individual (see text). Solid circles are individuals from protected sites and open circles are individuals from exploited sites. The scaling relationship is isometric for all individuals combined and separately for individuals from exploited and protected sites.

DISCUSSION

The range of size-classes within a species is of course much smaller than that found between species, but whether intra- versus interspecific scaling relationships (such as home range scaling) are significantly different has not been rigorously established. One reason for this is that ecological scaling relationships and resulting theory have primarily been studied for determinate growing endotherms – species in which body mass does not change much after maturity (Calder, 1984). Indeterminate growing ectotherms such as limpets are good study organisms for testing the concordance of intra- versus interspecific scaling relationships because individuals experience significant growth after maturity, allowing for a relatively large continuum of body mass and associated home range measurements (Fig. 2). For example, body mass varies by more than an order of magnitude across *L. gigantea* individuals (Fig. 2), allowing for good resolution of intraspecific scaling relationships.

Here, I show that the isometric home range scaling relationship often reported for interspecific studies of terrestrial endotherms is also found on the intraspecific scale for an ectothermic marine invertebrate. These results suggest that isometric home range scaling may be a common property of species spanning different levels of biological organization, from individuals to species and across thermoregulation categories – not to mention the terrestrial versus marine divide and the vertebrate versus invertebrate phylogenetic gap. Although I only present data for one species, the same reasoning suggested to cause home range isometry across endothermic species could also apply to *L. gigantea.*

For mammals, observed home range scaling isometry is partially explained by metabolic requirements, which dictates that individual food requirements scale with metabolism at $\sim M^{0.75}$. However, home range area consistently scales larger than 0.75 across mammals,

which Jetz *et al.* (2004) demonstrate to be due to intraspecific competition for resources, causing space use overlap, smaller exclusivity of home range use, and ultimately a scaling exponent higher than 0.75 (i.e. ~1.0). Although slight differences in the exponent have been observed for different body sizes (Jetz *et al.*, 2004; Marquet *et al.*, 2005), trophic groups (Kelt and Van Vuren, 2001; Nilsen and Linnell, 2006), and by geographic region (Lindstedt *et al.*, 1986) across mammal species, the overall scaling trend is one of isometry (Jetz *et al.*, 2004; Marquet *et al.*, 2005; Woodward *et al.*, 2005). Herbivorous mammals tend to show a pattern most consistent with isometric scaling (Kelt and Van Vuren, 2001; Jetz *et al.*, 2004), which is suggested to be related to a more uniform availability of food resources compared with other groups, such as carnivores (see Kelt and Van Vuren, 2001 and references therein).

Although the mechanistic processes leading to home range isometry require further study, the intraspecific space use overlap hypothesis suggested to contribute to home range isometry in mammals (Jetz *et al.*, 2004) might also apply to *L. gigantea*. The medium to large individuals in *L. gigantea* populations tend to be female who patrol a territory while grazing on a thin algal layer (i.e. her 'garden': Fig. 1). Peripheral non-territorial individuals (generally male) periodically raid the territory and eat as much as they can before being 'bulldozed' away (Schroeder, 2011). Thus, territorial raids would be considered intraspecific space use overlap in a similar manner suggested for mammals and could account for the home range scaling concordance between such divergent phylogenetic groups.

More field studies and meta-analyses of existing data are needed on the intra- and interspecific scales for mobile marine ectotherms (e.g. gastropods) to determine whether home range isometry is indeed a general pattern that transcends marine and terrestrial habitats and thermoregulation categories. Examples of home range/territoriality studies for marine species do exist (e.g. Kramer and Chapman, 1999; Pittman and McAlpine, 2003), but they often do not relate or present such data in a manner that allows for comparison with species for which ample data and theory exist (e.g. terrestrial endotherms) (but see Alimov, 2003). A broader variety of studies can be used: (i) to more fully test/adjust existing theory (Jetz *et al.*, 2004; West and Brown, 2005), (ii) to help identify the role of home range scaling in structuring marine communities, and (iii) to determine whether geographic variation in water temperature affects ectothermic scaling relationships.

Perhaps the most compelling reason for more studies is to assess if home range scaling and its influence on ecological communities is affected by human impacts. Increasing evidence shows that humans are causing a general reduction in the body sizes of species inhabiting marine and terrestrial habitats across the globe. The most commonly cited causes are size-selective harvesting/overharvesting (Fenberg and Roy, 2008) and, more recently, global climate change (Sheridan and Bickford, 2011). Whether individual home ranges are reduced for affected species is not in doubt judging by the lack of the largest space occupiers in exploited populations (e.g. Fig. 2) – which can have cascading ecological effects on communities (Fenberg and Roy, 2008). But whether the underlying scaling relationship is statistically different for impacted species is a question that should be more fully studied in order to understand and potentially mitigate the ecological and evolutionary consequences of reduced body size on individual species and their communities.

ACKNOWLEDGEMENTS

This work was supported by an EPA STAR Fellowship. I would like to thank Kaustuv Roy, Marcelo Rivadeneira, David Lindberg, Joshua Kohn, Russell Lande, Paul Dayton, David Holway, and Walter Jetz for valuable conversations about this study. Special thanks to the National Park Service and the University of California Reserve System for research permission at Cabrillo National Monument and the Kenneth S. Norris Rancho Marino Reserve.

REFERENCES

Alimov, A.F. 2003. Territoriality in aquatic animals and their sizes. *Biol. Bull.*, **30**: 79–86.

Anderson-Teixeira, K.J., Savage, V.M., Allen, A.P. and Gillooly, J.F. 2009. Allometry and metabolic scaling in ecology. In *Encyclopedia of Life Sciences (ELS)*. New York: Wiley.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. and West, G.B. 2004. Toward a metabolic theory of ecology. *Ecology*, **85**: 1771–1789.

Calder, W.A. 1984. *Size, Function, and Life History*. Cambridge, MA: Harvard University Press.

Fenberg, P.B. and Rivadeneira, M.M. 2011. Range limits and geographic patterns of abundance of the rocky intertidal owl limpet, *Lottia gigantea. J. Biogeogr.*, **38**: 2286–2298.

Fenberg, P.B. and Roy, K. 2008. Ecological and evolutionary consequences of size-selective harvesting: how much do we know? *Mol. Ecol.*, **17**: 209–220.

Fenberg, P.B. and Roy, K. 2012. Anthropogenic harvesting pressure and changes in life history: insights from a rocky intertidal limpet. *Am. Nat.*, **180**: 200–210.

Hendriks, A.J. 2007. The power of size: a meta-analysis reveals consistency of allometric regressions. *Ecol. Model.*, **205**: 196–208.

Jetz, W., Carbone, C., Fulford, J. and Brown, J.H. 2004. The scaling of animal space use. *Science*, **306**: 266–268.

Kelt, D.A. and Van Vuren, D.H. 2001. The ecology and macroecology of mammalian home range area. *Am. Nat.*, **157**: 637–645.

Kido, J.S. and Murray, S.N. 2003. Variation in owl limpet *Lottia gigantea* population structures, growth rates, and gonadal production on southern California rocky shores. *Mar. Ecol. Progr. Ser.*, **257**: 111–124.

Kramer, D.L. and Chapman, M.R. 1999. Implications of fish home range size and relocation for marine reserve function. *Environ. Biol. Fishes*, **55**: 65–79.

Lindberg, D.R., Estes, J.A. and Warheit, K.I. 1998. Human influences on trophic cascades along rocky shores. *Ecol. Appl.*, **8**: 880–890.

Lindstedt, S.L., Miller, B.J. and Buskirk, S.W. 1986. Home range, times, and body size in mammals. *Ecology*, **67**: 413–418.

Makarieva, A.M., Gorshkov, V.G. and Li, B.L. 2005. Why do population density and inverse home range scale differently with body size? Implications for ecosystem stability. *Ecol. Complex.*, **2**: 259–271.

Marquet, P.A., Quinones, R.A., Abades, S., Labra, F., Tognelli, M., Arim, M. *et al.* 2005. Scaling and power-laws in ecological systems. *J. Exp. Biol.*, **208**: 1749–1769.

Nilsen, E.B. and Linnell, J.D.C. 2006. Intra-specific variation and taxa-sampling affects the home range body mass relationship. *Acta Theriol.*, **51**: 225–232.

Pittman, S.J. and McAlpine, C.A. 2003. Movements of marine fish and decapod crustaceans: process, theory and application. *Adv. Mar. Biol.*, **44**: 205–294.

R Development Core Team. 2012. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Sagarin, R.D., Ambrose, R.F., Becker, B.J., Engle, J.M., Kido, J., Lee, S.F. *et al.* 2007. Ecological impacts on the limpet *Lottia gigantea* populations: human pressure over a broad scale on island and mainland intertidal zones. *Mar. Biol.*, **150**: 399–413.

Schroeder, S.L. 2011. The behavioral ecology and territoriality of the owl limpet, *Lottia gigantean*. PhD dissertation, University of Oregon, Eugene, OR.

Shanks, A.L. 2002. Previous agonistic experience determines both foraging behavior and territoriality in the limpet *Lottia gigantea* (Sowerby). *Behav. Ecol.*, **13**: 467–471.

Sheridan, J.A. and Bickford, D. 2011. Shrinking body size as an ecological response to climate change. *Nature Climate Change*, **1**: 401–406.

Sibly, R.M., Brown, J.H. and Kodric-Brown, A., eds. 2012. *Metabolic Ecology: A Scaling Approach*. Oxford: Wiley-Blackwell.

Stimson, J. 1970. Territorial behavior of the owl limpet, *Lottia gigantea. Ecology*, **51**: 113-–118.

West, G.B. and Brown, J.H. 2005. The origin of allometric scaling laws in biology from genomes to ecosystems: towards a quantitative unifying theory of biological structure and organization. *J. Exp. Biol.*, **208**: 1575–1592.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A. *et al.* 2005. Body size in ecological networks. *Trends Ecol. Evol.*, **20**: 402–409.

Wright, W.G. 1989. Intraspecific density mediates sex-change in the territorial patellacean limpet, *Lottia gigantea. Mar. Biol.*, **100**: 353–364.