

THOMAS HENRY HUXLEY REVIEW

Patchwork planet: the resource dispersion hypothesis, society, and the ecology of lifeD. W. Macdonald¹ & D. D. P. Johnson²¹ Wildlife Conservation Research Unit, The Reanati-Kaplan Centre, Department of Zoology, University of Oxford, UK² Department of Politics and International Relations, University of Oxford, UK**Keywords**

RDH; group size; territory size; sociality; cooperation; spatial; temporal; home-range; resource dispersion hypothesis.

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Abstract

Virtually nothing in nature is uniform. Observed at the right scale, most entities are clustered rather than evenly distributed, spatially and temporally, and this applies across domains from the distribution of matter in the universe, to habitats across the Earth's surface, and to energy in the landscape. Patchiness means organisms cannot carve out even territories. Instead, their shape and size depends on the dispersion of materials needed for survival and reproduction. This fundamental feature of life is intrinsically understood in ecology, for example, in the ideal free distribution and optimal foraging theory, and is represented in the anatomy as well as behaviour of organisms via the structures and strategies for moving, finding and capturing these patchy resources. But perhaps most striking of all is the role of patchiness in facilitating the formation of social groups – of societies. The resource dispersion hypothesis (RDH) suggests that where resources are dispersed and rich enough, multiple individuals can collapse into groups that share the same space at little cost to each other. Cooperation may be absent, but sociality is favoured nevertheless. Thirty years after the origin of the hypothesis, we review the accumulating models, critiques, evidence and experiments, concluding that RDH is a pervasive feature of animal spacing patterns across a wide range of species, taxonomic groups and ecosystems. In the spirit of the original objective of the Huxley Reviews to 'suggest and inspire research that will improve our knowledge in the future', we also take the opportunity to consider wider implications of the RDH. If we live and evolved on a patchwork planet, then we should expect broader effects. Indeed, we suggest that the RDH has played an important role in the evolution of cooperation, biodiversity, behaviour and, not least, in the social organization of humans in our evolutionary past and today.

Introduction

The 1960s and 1970s saw a revelation in understanding the adaptive significance of animal societies in terms of ecological selective pressures. John Crook's (1964) categorizing of weaver bird society in terms of different types of seed source, followed by an ecological explanation of primate societies (Crook & Gartlan, 1966), set the pace for Jarman's (1974) linkage of antelope sociology to the characteristics of the vegetation on which they fed. These early explorations interpreted ecological circumstances with a broad brush (Crook, 1964; Crook & Goss-Custard, 1972; Jarman & Jarman, 1973, 1974; Crook, Ellis & Goss-Custard, 1976; Jarman, 1979), but were soon followed by more subtle teasings apart of the impacts of resources on interspecific (e.g. Clutton-Brock, 1974) and intraspecific (Kruuk, 1972) variation in societies. As attention turned to the intricacies of

why animals live in groups, Kruuk (1978a,b) drew attention to the existence of some carnivore societies that were not obviously explained by cooperation. Badgers, *Meles meles* and foxes, *Vulpes vulpes*, provided variations on this theme (Kruuk, 1978b; Macdonald, 1981), as did a seminal series of four papers on bats by Bradbury & Vehrencamp (1976a,b, 1977a,b). Much influenced by these, Macdonald (1983), in a paper entitled 'The ecology of carnivore social behaviour', crystallized these ideas into an ecological explanation for group living, naming it the resource dispersion hypothesis (RDH). The nub of RDH is that groups may develop where resources are dispersed such that the smallest economically defensible territory for a pair (or whatever is the basic social unit) can also sustain additional animals (Macdonald, 1983). Whether these additional animals opt to join the group will depend on their tolerance of the variation in surplus resources (residual food security), and on the pros

and cons of joining versus leaving. But here was a mechanism to explain how spatial groups can form even where cooperation or other benefits of group living are absent.

As well as providing an explanation for why individuals may sometimes coalesce into groups in shared spaces, the RDH offered a foil to debate the interaction of ecology and behaviour in the evolution of sociality. RDH suggests that you do not need behavioural interactions to explain the origins of groups. Since first proposed, the RDH has been widely examined, and has accumulated broad support among a variety of species, habitats, taxonomic groups and types of resources. We synthesize this support here, which has accelerated in recent years, as well as developing the broader insights of the RDH for biodiversity, ecology, human evolution and social science.

RDH theory

Axiomatically, group living evolves when the net benefits of association with other conspecifics in the group exceed the costs (Alexander, 1974). Thus, group living is theorized to evolve when the fitness benefits obtained by an individual in joining a group outweigh the costs of sharing key resources with conspecifics (Macdonald & Carr, 1989; Bacon, Ball & Blackwell, 1991a,b; Koenig *et al.*, 1992; Cockburn, 1998; Hatchwell & Komdeur, 2000; Johnson *et al.*, 2002b) and/or when there are strong ecological constraints on reproducing independently of the group (see von Schantz, 1984b; Lindstrom, 1986; Hatchwell & Komdeur, 2000). The selective advantage of group living is often obvious in terms of increased vigilance, foraging capacity, cooperative activities or reduced reproductive costs (Krause & Ruxton, 2002). But living in groups can also involve costs, such as greater risk of infectious disease, or heightened competition. Natural selection must therefore weigh the costs and benefits of sociality; but when the benefits predominate, animals will tend to congregate (or, equally, when the costs of going it alone are too high, which reminds us that the benefits could be low, but better than the alternatives). This is reviewed for carnivores in Creel & Macdonald (1995; see also Cahan *et al.*, 2002; Macdonald *et al.*, 2004b; Macdonald *et al.*, 2010), but in the context of carnivores, Kruuk (1978b) was the first to highlight that badger society presents a paradox: although at higher densities they live in conspicuously sociable groups, they display minimal cooperation or other behavioural benefits of group living (Macdonald, 1983; Kruuk & Macdonald, 1985; Woodroffe & Macdonald, 1993). RDH offers a solution to this paradox, which applies not just to badgers, but generally. Indeed, we argue it sheds light on many vertebrate societies, including those of people. Since resource dispersion is a fundamental feature of ecology, then we should not be surprised that it applies broadly.

What is the RDH?

As progressively synthesized by Carr & Macdonald (1986), Bacon *et al.* (1991a,b) and Johnson *et al.* (2002b), the RDH is an hypothetical model that proposes that, where resources are

Box 1 The binomial version of the RDH

Imagine a game in which one die is a food patch and one throw determines the food available for one night. Let's say we can eat only if we throw a '6', and that throwing a '6' secures enough food for one animal for that night. Obviously, having six sides, one die gives a 1/6 or 16.7% chance of eating. It would be imprudent to gamble your fortunes, far less fitness, on such low odds. Given the choice, you might refrain from joining the game unless you had, say, at least an 80% security of eating each night, that is, an 80% chance of throwing a '6'. How many food patches, or dice, do you need to secure this level of food security? Because each six-sided die carries 5/6 chance of failure you need nine dice for 80% food security [$1 - (5/6)^9 = 0.806$]. Of course, the principle is obvious: that having secured the nine dice needed in order to eat at all on 80% of nights, on many nights extra '6s' will be thrown, on which it is possible for primary occupants to share the territory with secondary occupants at little or no cost to themselves. This is the binomial (that is, all or nothing) version of RDH proposed by Carr & Macdonald (1986). It illustrates how groups may develop where resources are dispersed such that the smallest economically defensible territory for a pair, which we refer to as a 'minimum territory', can also sustain additional animals – in the dice game, feeding periods during which more than one '6' is thrown.

patchily distributed over space and/or time, the economics of exploiting these patches enable several individuals to share resources over a common area, provided they can all satisfy their resource needs without imposing unsustainable costs on each other (Box 1; Fig. 1). The resulting social unit, in its least structured form a 'spatial group', can be durable, and thus distinct from the ephemeral aggregations of, for example, bears at a salmon leap or vultures at a carcass (although these phenomena can also reflect the broader RDH principle of groups forming around rich patches, see Table 2 later). The basic idea is that even a single animal (or, more plausibly, the basic social unit, be it a pair or larger group) using patchy resources will have to defend a large enough area to be sure that, with some critical probability, at least one 'ripe' patch will be available to satisfy its resource requirements over a given time period. This same area supporting the original resident(s) ('primary occupant(s)') is predicted to have an excess of resources at least some of the time, so that there might often be sufficient resources to sustain additional animals ('secondary occupants'). Although these additional animals might experience a lower level of food security than the original residents, the RDH mechanism posits that the resource-based cost of sharing a territory is acceptable, without reducing (much or at all) the fitness of either the primary or secondary individuals (see Table 1). There is a

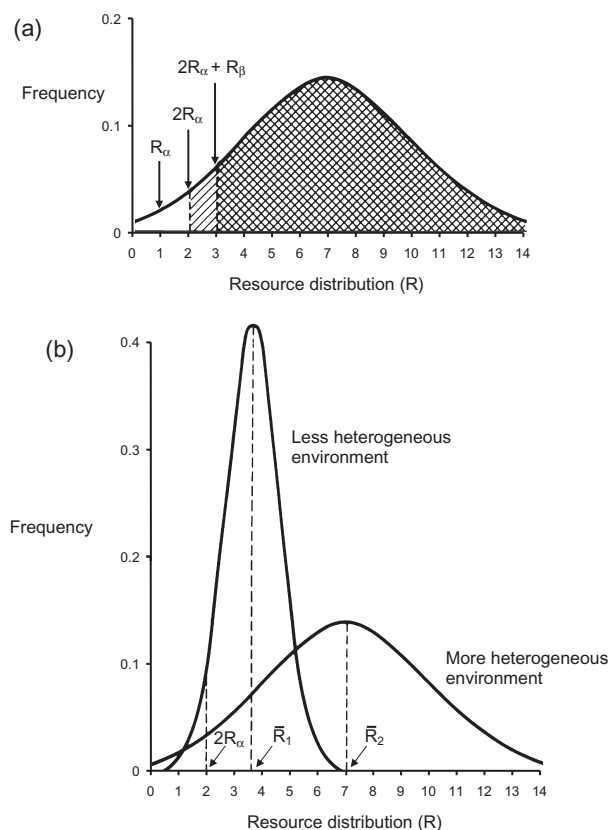


Figure 1 How the resource dispersion hypothesis works. (a) If resource patches have a certain probability of availability, then several must be simultaneously defended to guarantee some probability of finding enough food for a primary pair of residents ($2R_\alpha$) in a given period. A frequency distribution of availability across all patches (here, arbitrarily, $n = 1-14$) indicates the proportion of nights on which the total amount of resources available will exceed $2R_\alpha$. A secondary can join the territory when their own resource needs (R_β) are met on top of those of the primaries (i.e. $2R_\alpha + R_\beta$). The integral of the distribution illustrates the 'critical probabilities' (Cp), the proportion of times that such conditions occur for primaries [$Cp_\alpha = 0.95$ (upward hatching)] and secondaries [$Cp_\beta = 0.90$ (downward hatching)]. Wherever these two distributions overlap (i.e. the cross-hatched area), both primaries and secondaries attain their food requirements. Changing the shape of the distribution will not alter R_α and R_β , but it will alter the critical probabilities associated with them, leading to a different prediction for group size. (b) Two superimposed graphs, similar to that in a. The taller curve represents a territory in a relatively invariable environment with a low mean resource availability (\bar{R}_1). The flatter curve, by contrast, corresponds to a territory in a more variable environment with a higher mean resource availability (\bar{R}_2). The area under each curve is the same (1.0), and represents the total probability of all the possible levels of availability. In both cases, each curve represents the distribution of resources from the minimum territory required to satisfy a given Cp_α . The crucial difference is that Cp_β (the probability of achieving $2R_\alpha + R_\beta$) is much higher with the flatter curve (90%) than with the taller curve (72%), so secondary animals are more easily supported in the more heterogeneous environment. More variable environments will, therefore, be able to support larger group sizes. Reproduced, with permission, from Carr & Macdonald (1986).

variety of circumstances under which these conditions could prevail, but a binomial version of this idea is easily envisioned as a game of dice (See Box 1).

In extremis, therefore, the RDH explains how some species could live in groups even without there being any other evident functional benefits (e.g. no cooperative hunting, alloparental care or predator defence) from doing so. More importantly, it describes ecological conditions that can kick-start sociality by enabling animals to cohabit at little or no cost, thereby facilitating the subsequent evolution of cooperative behaviour that further pushes the cost-benefit balance towards sociality. This suggests two pathways by which RDH influences the evolution of sociality. First, resource distributions may have provided a ladder for a species to establish groups, and these groups may persist or entrench once the ladder has been kicked away (even if, for example, resource distributions subsequently change and are no longer patchy). Group life may then endure for other functional reasons, but which resource dispersion permitted to emerge. Second, resource distributions may stay the same, thus remaining an important aspect of the social scaffolding whether there are other functional benefits of group life or not. This has implications for conservation, behaviour and disease dynamics: change the ecology and you may unhinge sociality.

Expansionists and contractionists

Of course, where ecological conditions facilitate the formation of spatial groups, or even where they don't, the many advantages of cooperation can make group living advantageous. The RDH neither discounts nor precludes the possibility that animals may strive to maintain territories and/or groups that are larger than the minimum. The absolutely greater (but proportionately lesser) costs of border defence for the territorial expansion required to support larger groups might be offset by its benefits. These could be direct benefits such as greater reproductive potential. But there may be indirect benefits as well. For one thing, secondaries can be related to primaries, so that costs of group defence are mitigated as a function of the coefficient of relatedness (r), and benefits correspondingly elevated. In the calculus of whether there is marginal benefit (to primaries or secondaries) for secondaries to remain or disperse (Macdonald & Carr, 1989), are all the factors that affect the odds of natal philopatry (e.g. Waser & Jones, 1983), including kin selection (von Schantz, 1984c), cooperative breeding and delayed dispersal (Kokko & Ekman, 2002). Where the conditions of RDH prevail, capitalizing on the sociological benefits of group living comes free (or cheap) to members of a spatial group occupying the minimal defensible territory. Whether these advantages are so great as to make it advantageous to expand the group to a size that requires a territory larger than the minimum necessary for the basic social unit, or whether the advantage of larger group size does not subsidize expansion beyond that minimum, leads to Kruuk & Macdonald's (1985) concept of expansionism versus contractionism, which is inextricably linked to understanding the ramifications of RDH.

Table 1 Effects of variation in key variables (all else equal) on primaries' and secondaries' food security and fitness (which are separated because fitness can be affected over and above changes in food security alone)

If there is an increase in:	Effect on primaries'		Effect on secondaries'	
	Food security	Fitness	Food security	Fitness
Heterogeneity (H)	+	+	+	+
Patch dispersion (PD)	=	– ^a	=	– ^a
Patch richness (PR)	+	+	+	+
Patch number (or renewal rate)	+	+	+	+
Territory size (TS)	= ^b	– ^b	= ^b	– ^b
Group size, i.e. more secondaries (GS)	= ^c	+/ ^d	–	–
Primaries' food demands (R_{α})	+	+	+ ^e	+ ^e
Secondaries' food demands (R_{β})	=	=	–	–
Territory defense costs	=	–	=	–
Proportion of kin in the group	=	+	=	+

The symbol '+' means food security or fitness increases, '–' means they decrease and '=' means they are unaffected. The point of the table is to highlight that some variations affect primaries and secondaries similarly (e.g. increasing the richness or number of patches), and thus favour group cohesion, while other variations affect them differently (e.g. group size and secondaries' food demands) and thus favour group fission. In the latter cases, secondaries are worse off, although having related individuals in the group can subsidize fitness losses.

^aTravel costs increase to maintain the same level of food security.

^bDefence costs increase without any necessary gains (more territory may not include any more patches).

^cUp to a point (as defined in Fig. 1).

^dDepending on whether the presence of secondaries bring other costs or benefits (e.g. competing for mates, but helping with defence).

^eThis may seem counter-intuitive, but if primaries have greater food demands, then they must occupy a more productive territory, with greater potential surpluses for secondaries. (The reverse is not true: if secondaries have greater food demands, they are less able to join or stay in a given primary's territory).

An expansionist tends to increase the size of its territory, in excess of minimal requirements for breeding, up to some asymptote at a species- or habitat-specific optimum. Therefore, all else being equal, the territory owners who can draw on the greatest corporate strength (e.g. the strongest or largest group) will occupy the largest range. A contractor will maintain the smallest economically defensible area, which will encompass sufficient resources for reproduction (Brown, 1964), so a group of contractors can only develop where the distribution or availability of resources are such that this smallest range can, at least sometimes, support a larger group (viz. RDH). There may be many ways in which these conditions arise for contractionists including, as we elaborate below, commonly where food or other resources are spatio-temporally patchy (Carr & Macdonald, 1986), but also cases where there are purely temporal variations in resource availability (von Schantz, 1984b) or favourable patterns of renewal of resources (Waser, 1981). Kruuk & Macdonald (1985) illustrated the principle by the possibility that the territory size of spotted hyaena, *Crocuta crocuta*, is determined by the average distance over which they chase prey, such as wildebeest; the smallest territory, which would allow even one hyaena the space needed to overhaul a wildebeest supports sufficient prey to sustain many hyaena.

Territory holding is often an adaptation to defend a limiting resource, usually food (e.g. Brown, 1964; Davies & Houston, 1981). Since territoriality involves costs (e.g. time and energy defending it from conspecifics) as well as benefits, theory predicts that territories will generally not be larger than the minimum size required to satisfy the requirements of all

the occupants (insofar as further enlargement would bring extra costs without net benefits). Under the circumstances described by RDH, secondary animals can cohabit with the primary occupants at little or no cost (Carr & Macdonald, 1986; Blackwell & Macdonald, 2000; Johnson & Macdonald, 2003). The 'cost' to these secondary animals has been debated (Woodroffe & Macdonald, 1993; Revilla, 2003a,b); it need not be cost-free (cf. Roper, 2010), but must be both bearable and less expensive than other sociological options (see Carr & Macdonald, 1986; Baker *et al.*, 2004; Newman *et al.*, 2011). Group living, however, inevitably leads to competition between group members for access to limited resources (e.g. mates, food and breeding sites) and variation in the availability and distribution of these resources might therefore influence the rewards of tolerance and marginal values of group membership (Macdonald & Carr, 1989; Kokko & Rankin, 2006; Silk, 2007; Huchard & Cowlshaw, 2011; see Table 1).

Sources of variation

So, the RDH would not necessarily expect (even in broadly similar habitats) any relationship between group size and territory area, as the two are argued to be affected, largely independently, by the abundance and dispersion of available food (Mills, 1982; Macdonald, 1983). For a given patch richness (the amount of food available when that patch is ripe), however, one would expect territory area to be larger where patches are more dispersed – that is, fewer patches per unit area (see table of predictions in Johnson *et al.*, 2002b). Furthermore, Carr & Macdonald's (1986) binomial model

makes clear that there are three environmental parameters that determine the probability with which additional group members can be sustained in the territory. These are richness, heterogeneity, and renewal (see Table 1). All else being equal, the costs to primary occupants of tolerating additional group members in their territory will be diminished (along with levels of deprivation that secondaries need to tolerate) if we (1) increase patch richness (that is, the total amount of food available); (2) increase heterogeneity (e.g. by lowering the likelihood that any one throw of the die will be fruitful, for example, by moving from conditions where throwing either 5 or 6 is fruitful to conditions where only a six yields food); or (3) increase renewal rate (by throwing the dice more often per feeding period). The influence of resource renewal rate on the rewards of tolerance (Macdonald & Carr, 1989) was convincingly argued by Waser (1981), who developed a model that predicts the costs of tolerating conspecific foragers as a function of a predator's rate of harvesting prey and the prey's renewal rate. These predictions were consistent with patterns of social grouping observed in small African carnivores such as most mongooses and viverrids. Of course, the larger the absolute value of the food security demanded by the primaries, and the more tolerant the secondaries are to deprivation, or the lower their relative requirements, the more likely it is that secondaries can be accommodated (Table 1).

Demands and consequences

This theme is developed in a comparison of the behavioural ecology of two mustelid carnivores by Newman *et al.* (2011), who suggest that body size and shape mediates the relationship between food resources and sociality differently for martens (which live solitarily) and Meline badgers (which form groups). The rotund body type of badgers predisposes them to tolerating restricted food security, by buffering periods of scarcity with increased body mass. Badgers also use torpor to cope with seasonal food scarcity, and conserve energy by remaining within complex subterranean dens. Furthermore, their ability to store body fat enables them to hibernate, in harsher parts of their range, through food-scarce winter seasons. Martens, in contrast, must maintain a lean, elongate body type for effective hunting and thus do not store energy as increased body mass to a comparable extent. Martens do not exhibit torpor, their dens are simple and they do not hibernate; indeed, they typically cannot tolerate more than 72 h without food (by contrast, badgers have been recorded not emerging from their setts for several weeks; Newman *et al.*, 2011). They conclude that these differences preclude martens from tolerating restricted food security and thus, within an RDH framework, lowers the odds that the minimum territory defensible by the basic social unit could accommodate secondaries with lower food security, whereas these conditions are readily met by corpulent badgers (see Table 3 for this and other factors that make RDH more or less likely to enable group formation).

Note that this phenomenon can be generalized. For example, males are generally bigger than females, hence they

need a larger territory. Often, male territories have multiple females' territories within them (e.g. among various mustelids deer, and primates). Tolerating such 'secondaries' is not as costly as heretofore implied because they bring significant fitness advantages as mates. This may seem an obvious point. However, it has big consequences. Broad classes of mating systems hinge on the distribution of females, and by extension, the underlying distribution of food around which females space themselves (Davies, 1991). Thus, RDH may play a significant role in what kinds of mating systems emerge, or are even possible in a given environment, or in a given trophic niche (Yamaguchi & Macdonald, 2003). For similar reasons, the age of primaries and secondaries matters: young or old individuals will have a different level of food tolerance, and varying degrees of current and future benefits from having conspecifics of different age classes around.

Resource types: variations on the theme

Carr & Macdonald (1986) and Johnson *et al.* (2002b) are among those to highlight that the principle behind RDH can be expressed through many variants (with key types outlined in Table 2). For a start, while much focus is on food resources, the idea can apply to any resource, or combination of resources, including water, den sites, shelter and mates [and as noted above on mating systems, it seems common for the spatial organization of females to be around food, and that of males to be around females (Lukas & Clutton-Brock, 2013), as Kaneko *et al.* (2014) illustrate for the Japanese badger (*Meles anakuma*) and as generally described by Emlen & Oring (1977) and Davies (1991)]. Regarding patches, as Carr & Macdonald (1986) demonstrated, RDH can apply where they are numerous and each is less than a full meal, or where a single one is rich enough to satiate several individuals [a patch of earthworms may feed several badgers, and an elephant calf will feed several lions (Loveridge *et al.*, 2006)]. Similarly, while the hypothesis is often expressed in terms of clearly defined resource patches, it applies equally to contours of resource availability, and while it is often applied in terms of spatio-temporal variability, it accommodates equally temporal variation alone. Indeed, in an important paper, Paul Blackwell shows that, while people have tended to focus discussions around 'patches', the logic of RDH holds if we simply consider resources as being spatially correlated (Blackwell, 2007). Thus, the primary occupants of a territory encompassing even homogeneously dispersed prey, or a single rich patch, could form an RDH territory if prey availability varied seasonally or inter-annually. This was the scenario envisaged by von Schantz (1984a,b,c) for red foxes hedging their bets to configure territories to accommodate the bottleneck years over 3-year rodent cycles. von Schantz (1984a) referred to this as the 'constant territory size hypothesis' (CTSH), and described the behaviour of the foxes planning for the trough year 'obstinate strategists' [under the alternative 'flexible strategy' territory size varies seasonally with resources (e.g. access to females for males)]. Macdonald (1984) and Carr & Macdonald (1986) acknowledged the importance of the CTSH but identified it as a temporal extreme within the wider

Table 2 Alternative variants of RDH

Model	Spatial clustering	Temporal clustering	N resources clustered	Resource access	Effect	Example
Null model	No	No	None	Space is divisible	Individual territories	Petri dish
RDH type I	Yes	Yes	One/many	Enough patches must be incorporated in home range to ensure food security	Shape and size of home range of any organism, even if no secondaries	All species
RDH type II ^a	Yes	No	One	Resource hotspots	Congregations	Waterholes
RDH type III ^b	No	Yes	One/many	Resources vary seasonally	Migration	Arctic tundra
RDH type IV ^c	Either/or	Either/or	One	Resources vary daily, weekly, or monthly	Spatial groups	Food patch
RDH type V ^d	Either/or	Either/or	Many	Resources vary daily, weekly, or monthly	Spatial groups	Food + water + shelter
RDH type VI	Either/or	Either/or	One/many	Resources shared	Cooperative groups	IKung Bushmen
RDH type VII	Either/or	Either/or	One/many	Resources traded	Cooperative groups	Pitcairn Islanders

RDH Type 1 highlights the point that, given variation in the spatio-temporal availability of resources, all organisms must configure their territories to achieve some level of food security (as specified in Fig. 1), whether they are solitary or social. All other types of RDH fit our earlier definition: 'where resources are patchily distributed over space and/or time, the economics of exploiting these patches enable several individuals to share resources over a common area, provided they can all satisfy their resource needs without imposing unsustainable costs on each other.' RDH may be seen as being imperialistic here, claiming novel explanations for long-established phenomena (e.g. feeding congregations, migration). However, we see RDH as a unifying framework for understanding when organisms do (and do not) form spatial groups on the basis of underlying ecology, irrespective of spatial or temporal scale (hence seasonal as well as daily ranging behaviour), or how resource patches are accessed (hence also sharing and trade). If RDH diverged from, or could not explain, congregations, migration, multiple resource types, sharing, and trading, among other phenomena, then it would be a less parsimonious theory.

^aThis might not seem like RDH, however, the variables are in place: Resources are spatially dispersed and individuals must include enough such 'patches' in their range to satisfy a given level of food security. Yet each patch, when available, is rich enough to support multiple individuals.

^bThis might not seem like RDH either, but again the variables are in place: Across the seasons, resources are spatially dispersed and individuals must include multiple resource locations in their annual range (e.g. winter feeding grounds, summer nesting habitat). Yet the convex polygon around these resources can include many other individuals.

^cThis is the classic, Carr & Macdonald (1986) version of RDH in which the distribution of patch availability allows (durable or permanent) home range overlap.

^dThis is exactly the same as Carr & Macdonald (1986) except that there are multiple sets of dice (one for each resource; see Box 1).

Table 3 Conditions that make RDH more or less likely to enable group formation in a given species or setting

Domain	Low chance of RDH	High chance of RDH	Explanation
Body size	Small	Large	Larger body size (and lower metabolism) increases tolerance of low food security
Life-history	r-selected	K-selected	Longer life span increases capacity to incur short-term costs for long-term gains (e.g. sharing territory or low food security)
Niche	Generalists	Specialists	Specialist diet reduces choice of alternative prey or feeding areas (and thus increases reliance on the availability of a given set of resource patches)
Key resources	Few	Many	A greater number of limiting resources (e.g. patchy food and water and shelter) is more likely to compel home range overlap or tolerance of secondaries. (Note this does not work for multiple prey types, hence the opposite implication for niche generalists/specialists above)
Prey type	Small	Large	Larger prey more likely to represent concentrated patches of energy (though not always, since small prey can themselves be concentrated)
Body plan	Low body fat	High body fat	Greater body fat increases tolerance of low food security
Torpor	Absent	Present	Torpor/hibernation increases tolerance of low food security
Food caching	No	Yes	Caching food increases tolerance of low food security
Signalling	Absent	Present	Information transfer allows dispersed resource patches to be found and shared more efficiently, reducing food insecurity
Habitat	Homogenous	Heterogeneous	Diverse habitats more likely to yield patchy resources across space
Climate	Stable/predictable	Variable/unpredictable	Variable/unpredictable climate more likely to yield patchy resources over time

Each row represents a physiological, behavioural or environmental mechanism that alters the impact of spatial or temporal variation in resources. This may offer a starting point from which to examine whether there are taxonomic patterns in the effects of RDH among species and ecosystems. It may also suggest candidate species for which resource dispersion will be an especially important influence on territory or group size. Note that there are two counter-acting implications. Implication 1 is that, for primaries, territories can be smaller. This is because such factors (e.g. high body fat, torpor, food caching) can smooth out the effective spatial or temporal variation in resources, reducing the influence of resource dispersion on food security, since patchy energy availability in the environment can now be accessed more evenly by the animal. In principle, such animals may be able to achieve the same food security in a smaller area. Implication 2 is that, for secondaries, groups can be larger. This is because the same factors (e.g. high body fat, torpor, food caching) can increase their tolerance of low food security, allowing larger groups to form in a given area of patchy habitat. There are likely to be complex interactions between the implications for primaries and their minimum economically defensible territories and the ability of secondaries to squeeze into them.

family of RDH scenarios (see Table 2). Linked to cyclical prey, Lindstrom (1986) suggested that it pays primary occupants to maintain larger ranges during bottleneck years so that they can be partitioned among offspring during richer years (the 'territory inheritance hypothesis'; TIH). The TIH is sometimes advanced as an alternative to RDH but, as argued by Carr & Macdonald (1986), and as Blackwell & Bacon's (1993) modelling led them to conclude, the TIH requires RDH (or something equivalent) for it to work. In essence, the CTSH and TIH were alternative expressions of the underlying RDH formula, each highlighting one region of a wider parameter space within a more general framework.

The theory was significantly advanced when mathematician Paul Blackwell (1990) modelled RDH to determine when the strategy of exploiting an opportunity to form groups would be successful. In his model, which was stochastic and represented the system as a Markov chain, the state of the system depended not only on the number of users of each strategy but also on their organization into groups. Bacon *et al.* (1991a,b) produced a further model that supported the predictions of RDH.

Note that all 'types' of RDH in Table 2 fit our earlier definition (p. 76): 'where resources are patchily distributed over space and/or time, the economics of exploiting these patches enable several individuals to share resources over a common

area, provided they can all satisfy their resource needs without imposing unsustainable costs on each other.' For some sceptics, RDH will be seen as being imperialistic here, claiming novel explanations for long-established phenomena. We see it differently. RDH is a unifying framework for understanding when animals do (and do not) form spatial groups on the basis of underlying ecology. If it diverged from, or could not explain, congregations and migration as well as other phenomena, then it would be a less parsimonious theory.

Objections to RDH theory

Despite recurrent corroboration of the core idea, and the supportive conclusions of explicit models, RDH has received criticism from (1) those claiming it lacks falsifiable predictions, (2) those claiming it lacks empirical evidence, and (3) those who misunderstand the concept. Most criticisms arose soon after the RDH's formulation, and have since been resolved.

The RDH was initially criticized for lacking falsifiable predictions (von Schantz, 1984a), an objection which Macdonald (1984) argued was not correct. The RDH is a testable hypothesis, making clear predictions (e.g. see the table of multiple collated predictions in Johnson *et al.*, 2002b). Furthermore, in

combination, these predictions are unique and distinguish it from several alternative theories of social grouping. There are nuances depending on circumstances, but general RDH predictions include: (1) territory size (TS) is independent of group size (GS); (2) TS increases with distance and/or time between resource aggregations; (3) GS increases with an overall increase in patch richness (or renewal); and (4) GS increases with increased variability in the availability of resource aggregations (heterogeneity). The puzzle was not that the RDH lacks predictions, but why researchers did not rigorously test them. Johnson *et al.* (2002b) identified four reasons why RDH was often not applied or tested appropriately: (1) it was thought, erroneously, to lack testable predictions, (2) its effects can be masked by more obvious functional benefits of group living, (3) resource distributions are difficult to measure and (4) its assumptions and predictions were often misunderstood. Curiously, many studies that supported the RDH also did not do so through testing specific predictions, but rather by invoking it as the most parsimonious *a posteriori* explanation of the social spacing pattern observed. Much of this appears to result from people understanding, observing or testing different variants of RDH as distinguished in Table 2 (as well as issues of relevant spatial and temporal scales).

By 2003, Revilla (2003b) expressed surprise that in the 20 years since its first conceptual description, the RDH had not been modified [although in fact, various mathematical models had been formalized (Carr & Macdonald, 1986; Bacon *et al.*, 1991a,b)]. He argued that the large number of other hypotheses evoked to explain sociality constituted evidence that RDH had been considered as a weak (or unproven) explanation of group living by many authors, and led him to the conclusion that it was time to move beyond the RDH as a causal mechanism of group living (Revilla, 2003a). We suspect that the opposite is true: that the many explanations of group living are generally concordant with RDH, if not derivations of it, precisely because spatio-temporally heterogeneous resources are the norm, not the exception – hence our ‘patchwork planet’ concept. With regard to the evidence, the RDH may have lacked conclusive evidence at the time, but such a deficiency was due to a lack of good tests, rather than from the failure of tests (Johnson & Macdonald, 2003). Revilla saw a ‘conceptual gap’ between the RDH mechanism and a causal means of group formation because he incorrectly assumed that wherever resources are heterogeneous, RDH automatically predicts animals to live in groups. But as explained earlier, RDH is conceived as a facilitating, rather than a determining, factor leading to group formation. RDH cannot be rejected because it fails to explain all variants of sociality (e.g. it could not explain genetic eusociality among ants); nor because it is difficult to test. The RDH provides a heuristic tool with which to examine group living, and in accord with the principle of parsimony [or Ockham’s razor: ‘Plurality is not to be posited without necessity’ (Sober, 1981)], among competing hypotheses, it is often the most succinct and economic.

Prominent among the misunderstandings of the RDH concept are the criticisms of Roper (2010), who identified what he considered two important deficiencies of the RDH. First,

he observes that the nature of a food ‘patch’ has not been rigorously defined and varies in size and character between different studies evaluating the RDH. However, as we have seen, the RDH principle can apply to any form of heterogeneity (as now explained by Blackwell, 2007) and ‘patch’ is simply a convenient label to describe the concept of a mosaic of resources heterogeneous in space and/or time. Second, Roper states that a ‘major drawback of the RDH is that it is based on the idea that sociality in badgers is cost-free’. Again, this criticism is based on a simple misunderstanding of the precepts of the RDH – sociality is not ‘cost-free’ but rather a situation in which benefits (e.g. greater security) are more likely to outweigh the costs (e.g. sharing resources). As highlighted in Table 1, these may occur amidst many other factors, so a given identifiable cost does not mean sociality will not occur.

Although RDH describes patches that will sustain the group during a feeding period and so, by definition, incorporates patch depletion, and also deals with recovery from depletion by incorporating the rate of renewal, lack of appreciation of these aspects of the hypothesis has underpinned others’ criticisms (Johnson *et al.*, 2003). For instance, Buckley & Ruxton (2003) claim that an important assumption underlying both descriptive and mathematical representations of the RDH was missed – namely that the food supply from the territory in one foraging period is independent of the amount of food that was consumed in previous foraging periods (a better criticism would have been the issue of independence of patch richness within a feeding period). They conclude that considerations of the future value of food sources require reappraisal of the RDH in explaining the evolution and maintenance of group living. Renewal rates are, however, already implicitly or explicitly captured in parameters of the RDH model (e.g. in Carr & Macdonald, 1986; Bacon *et al.*, 1991b). Similarly, Barraquand & Murrell (2012) claim that resource depletion is unaccounted for in RDH models. This assumption leads them down an interesting but wayward road. They present a model that suggests that home-range size is related to total resource abundance. They conclude that the landscape abundance of resources is very important to the optimal home-range size for a consumer, and that the spatial segregation of consumer and resource is more important than the aggregation of the resource. In their model, the aggregation of resources only enters the feeding process indirectly, through its effect on the resource density and consumer-resource spatial correlation. They argue that depletion of resources tends to induce spatial segregation between consumers and resource. They conclude that further work is needed to decipher how much of the absence of a spatial aggregation effect can be attributed to our assumptions about the consumer foraging strategy (e.g. linear individual fitness), and to resource depletion that is ‘unaccounted’ for in RDH models. They also advocate the use of spatially explicit models incorporating feedbacks such as resource depletion in exploring evolutionarily stable foraging strategies, and show that for central place foragers, spatial aggregation effects might not happen as predicted by the RDH, again apparently missing the point that renewal rate and temporal heterogeneity are

incorporated into RDH. Their insights are important, but reflect aspects of the RDH universe rather than some other universe.

Finally, Kikvidze & Callaway (2009) dismissed RDH, proposing that ‘ecological facilitation’ can act as a cohesive force, and state that facilitative interactions that increase in intensity in stressful environments may explain the transition from solitary to group organization of populations. Insofar as RDH explains how resource dispersion facilitates group living, it is not clear why Kikvidze and Callaway (op. cit.) disallow it in their discussion of ecological facilitation. Once again, we appear to be in constant danger of reinventing the wheel, which is of course perfectly expected when we are presented with similar observations on a patchwork landscape.

Ten years ago, we concluded that despite its long history, there was little evidence to reject the RDH and a considerable amount of theoretical and empirical work to support it (Johnson & Macdonald, 2003). Indeed, it seems to have weathered its critics very well, and if anything, what is surprising is that there have been so few empirical tests providing evidence against it. Furthermore, at the time, while we reported steadily accumulating evidence in support of the RDH, now there is considerably more – including from a wide range of taxa and habitats, and also qualitatively more compelling types of evidence such as manipulation experiments, so support no longer rests on correlations.

Empirical evidence

We conducted an extensive review of the literature (Table 4) finding 65 studies with empirical support for the RDH and five against. These studies covered 43 species comprising a range of mammals, but also other taxonomic groups including birds, fish and crustaceans.

Much of the early inspiration for RDH stemmed from Hans Kruuk’s seminal thinking about badger sociality (e.g. Kruuk, 1978a,b). To put badgers in context, they belong to the Musteloidea, and this superfamily provides a rich array of species to which RDH seems relevant. As a broad generalization, all the terrestrial meat-eating musteloids are solitary, and the less that small mammals contribute to their diet, the more sociable musteloids tend to be (Macdonald, Newman & Harrington, in press). Terrestrial meat comes in packages that tend to be sparse, scattered across space (except in that large prey in themselves can represent a ‘patch’ that can be shared), slowly renewing and in need of defence. However, carnivores indulging in a mix of frugivory and carnivory and, especially, insectivory tend to live in larger groups (Creel & Macdonald, 1995).

In the case of the badgers of Wytham Woods (Oxfordshire), Kruuk conceived that the smallest economically defensible territory could be most simply modelled by the availability, dispersion and richness of patches of the badgers’ primary food source, the earthworm *Lumbricus terrestris*. While other food types (and indeed other resources) are also important to badgers – and they too contribute to territory geometry through their own dispersion – it is the sheer potential productivity (permitting super-abundant resources to be shared

with secondary group members) and the short-term volatility with which earthworm availability can change in response to optimal microclimatic conditions (Bouche, 1977; Kruuk, 1978a; Macdonald, 1983) that argues for their importance. In response to soil-surface micro-climate, in turn affected by the prevailing weather, habitat patches variously rich in earthworms become available to foraging badgers (Noonan *et al.*, 2014) in different habitats at different times (Da Silva, Woodroffe & Macdonald, 1993). When worm (and other seasonally important food resource) patches are irregularly shaped, widely dispersed and vary a great deal in nightly productivity, the minimum territory required by an individual badger will be more extensive and highly contorted, making it less sustainable to maintain exclusive access over these resources. Kruuk’s original principle was thus that, because each badger requires several blocks of worm-rich habitat to provide food reliably, it is the economics of resource dispersion that facilitate badger group formation by making it cost-effective to maintain less convoluted, more circular, territories that encompass food patches that are hard to partition but easy to share.

Badgers have remained a fruitful test-bed for RDH, and as Macdonald *et al.* (in press) conclude, no better hypothesis has yet emerged to explain badger groupings. Despite copious research, there is little evidence of cooperation among badgers (Dugdale, Ellwood & Macdonald, 2010), even mutual grooming is purely reciprocal and seemingly involves minimal trust (Macdonald *et al.*, 2000), and the integration of cubs into the group is driven by the cubs rather than the adults (Fell, Buesching & Macdonald, 2006). Even underground, badgers move about independently between sett chambers, with no clear affinities and come and go from the sett independently (Noonan *et al.*, 2014). Badger groups are also not exclusive breeding groups (Annabi *et al.*, 2014), with mating apparently occurring according to encounter rate, with half of cubs sired by males outside the group. This absence of alternative selective pressures for group living is clearly not direct evidence for RDH, but the exclusion of alternative hypotheses for badger sociality pushes the focus from sociological to ecological explanations. Certainly, at the regional level, as ecological circumstances change, so do badger social organization, group size and territory size as evidenced for example by great between-population variation across Europe (Johnson, Jetz & Macdonald, 2002a). Interdependence between ecological conditions and sociality is in evidence within sites as well. Da Silva *et al.* (1993) found that, in a natural experiment, land-use changes led to decreases in territory size with increasing patch richness, while reproductive success depended on patch richness. At Wytham, we subsequently constructed territory and habitat maps going all the way back to Kruuk’s work in the 1970s to test RDH predictions over a long time frame, using multiple alternative measures. Johnson *et al.* (2001) found that support for RDH predictions, for badgers, varied across years and depended on the method used to map territory borders. Across years, they found that TS was not consistently related to resource dispersion, nor was GS consistently related to resource richness, and suggested that more data were needed at different spatial scales of patchiness. The problem is

Table 4 Empirical support for RDH (in name order)

Species	Scientific name	Location	Type	Finding	Reference
African wild dog	<i>Lycan pictus</i>	South Africa (Kruger N.P.)	Field study	*HR correlated with PD (although authors reject RDH)	Mills & Gorman 1997
Alpine accentor	<i>Prunella collaris</i>	Pyrenees	Field experiment	Increase in PR increased effective GS (TS did not decrease)	Davies <i>et al.</i> 1995; Nakamura 1995
Antbirds	<i>Phaenostictus mcleannani</i>	Costa Rica	Field study	H (clumped ant colonies) associated with feeding groups	Chaves-Campos & DeWoody 2008
Arctic fox	<i>Alopex lagopus</i>	Svalbard	Field study	HR overlap correlated with PD and H	Eide, Jepsen & Prestrud 2004
Arctic fox	<i>Alopex lagopus</i>	Iceland	Field study	TS correlated with PD and GS correlated with PR	Hersteinsson & Macdonald 1982
Arctic fox	<i>Alopex lagopus</i>	North Pacific	Field study	TS unrelated to GS	Goltman <i>et al.</i> submitted
Badger	<i>Meles meles</i>	Norway	Field study	TS correlated with PD	Brosseth <i>et al.</i> 1997
Badger	<i>Meles meles</i>	UK	Natural experiment	Reduction in PD led to a reduction in TS, while PR correlated with number of breeding females and cubs	Da Silva <i>et al.</i> (1993)
Badger	<i>Meles meles</i>	UK	Field study	TS unrelated to GS; TS sometimes correlated with PD; GS sometimes correlated with PR	Johnson <i>et al.</i> 2002a,b
Badger	<i>Meles meles</i>	Japan	Field study	HR correlated with PD	Kaneko <i>et al.</i> 2014
Badger	<i>Meles meles</i>	UK	Field study	TS unrelated to GS; TS correlated with PD; GS correlated with PR	Kruuk & Parish 1982
Badger	<i>Meles meles</i>	Britain	Field study	Across the country, PD correlated with TS	Kruuk & Parish 1982
Badger	<i>Meles meles</i>	Scotland	Natural experiment	Decrease in PR associated with a (n.s.) reduction in GS, while TS remained the same	Kruuk & Parish 1987
Badger	<i>Meles meles</i>	UK (NE England)	Field study	TS correlated positively with PD, and negatively with PR	Palphramand, Newton-Cross and White 2007
Badger	<i>Meles meles</i>	Spain	Field study	*Contra RDH, TS correlated with PR rather than PD; males expansionist; individuals did not use all of HR (but see text for an RDH perspective)	Revilla & Palomares 2002
Badger	<i>Meles meles</i>	Spain	Field study	HR correlated with PD	Rodriguez, Martin & Delibes 1996
Badger	<i>Meles meles</i>	Portugal	Field study	HR correlated with PD	Rosalino, Macdonald & Santos-Reis 2004
Badger	<i>Meles meles</i>	Gloucestershire	By-product experiment	After a government cull, most territories reverted to same size	Tuytens <i>et al.</i> 2000
Badger	<i>Meles meles</i>	Gloucestershire	Field study	*TS weakly correlated with GS, but PD and PR not measured	Robertson <i>et al.</i> 2014
Bats	<i>Emballonurid spp.</i>	Costa Rica and Trinidad	Field study	TS correlated with patches of insect swarms; GS correlated with PR	Bradbury & Vehrencamp 1976b; 1976a
Bats	<i>P. pipistrellus</i> & <i>P. pygmaeus</i>	UK (NE Scotland)	Comparison	In two sympatric species, larger colony had smaller home ranges apparently due to PD	Nicholls & Racey 2006
Black kites	<i>Milvus migrans</i>	Africa and Europe	Field study	GS correlated with H and PR	Cortes-Avizanda <i>et al.</i> 2011
Black-footed ferrets	<i>Mustela nigripes</i>	USA (South Dakota)	Field study	HR correlated with PD	Jachowski <i>et al.</i> 2010
Blandford's fox	<i>Vulpes cana</i>	Israel	Field study	HR correlated with PD	Geffen <i>et al.</i> 1992
Cape clawless otters	<i>Aonyx capensis</i>	South Africa	Field study	HR correlated with PD	Somers & Nel 2004
Capybara	<i>Hydrochoerus hydrochaeris</i>	Venezuela	Field study	TS correlated with PD; GS correlated with PR	Herrera & Macdonald 1989
Chimpanzees and bonobos	<i>Pan troglodytes</i> & <i>Pan paniscus</i>	Africa	Field studies	Chimps focus on patchy fruit; bonobos also feed on ground vegetation	Wrangham, 1986
Coral-dwelling fish	<i>Paragobiodon xanthurus</i>	Papua New Guinea	Field experiment	GS correlated with PR	Thompson, Munday & Jones 2007
Coyotes	<i>Canis latrans</i>	Mexico	Natural experiment	PR (landfills) correlated with smaller TS and higher GS	Hidalgo-Mihart <i>et al.</i> 2004
Crab-eating foxes	<i>Caracyon thous</i>	Brazil	Field study	TS correlated with PD, and GS sustained by PR	Macdonald & Courtenay 1996
Dingos	<i>Canis lupus dingo</i>	Australia	Field study	HR correlated with PD, GS correlated with PR (though some long range forays into others' territories)	Newsome <i>et al.</i> 2013
Domestic cats	<i>Felis sylvestris</i>	UK	Field study	TS unrelated to GS	Macdonald 1983
Dunnocks	<i>Prunella modularis</i>	UK	Field experiment	TS increased and HRs overlapped when food provided in variable treatment	Davies & Hartley 1996
Eastern wild turkeys	<i>Meleagris gallapovo silvestris</i>	USA (Mississippi)	Field study	HR correlated with PD	Marable <i>et al.</i> 2012

Egyptian vultures	<i>Neophron percnopterus</i>	Africa and Europe	Field study	GS correlated with H and PR	Cortes-Avizanda <i>et al.</i> 2011
Ethiopian wolves	<i>Canis simensis</i>	Ethiopia	Field study	TS correlated with PD	Marino <i>et al.</i> , 2012.
Ethiopian wolves	<i>Canis simensis</i>	Ethiopia	Field study	GS correlated with H and PR	Tallents <i>et al.</i> 2012
European otter	<i>Lutra lutra</i>	UK	Field study	HR overlap around food and water patches	Kruuk & Hewson 1978; Kruuk <i>et al.</i> 1989
European shore crabs	<i>Carcinus maenas</i>	Ireland	Lab experiment	Groups formed in tank with clumped resources	Tanner & Jackson 2012
Giant otters	<i>Pteronura brasiliensis</i>	Manu N.P., Peru	Field study	GS correlated with PR	Groenendik <i>et al.</i> submitted
Gunnison's prairie dog	<i>Cynomys gunnison</i>	USA (northern Arizona)	Field experiment	HR overlap increased with increasing H (though GS did not change)	Verdolin 2009
Hairy-nosed otters	<i>Lutra sumatrana</i>	Cambodia	Field study	Spatial groups of females observed	Otter, 2003; Hwang & Larivière 2005
Kinkajou	<i>Potos flavus</i>	Panama	Field study	TS correlated with PD; GS correlated with PR	Kays & Gittleman 2001
Langurs	<i>Semnopithecus entellus</i>	Southern India	Field study	*GS negatively correlated with abundance of resources	Vasudev <i>et al.</i> (2008
Leopards	<i>Panthera pardus</i>	South Africa	Model	HR correlated with PD	Hayward <i>et al.</i> 2009
Lions	<i>Panthera leo</i>	Tanzania	Field study	HR unrelated to GS and correlated with PD	Spong 2002
Lions	<i>Panthera leo</i>	Zimbabwe	Field study	HR correlated with PD (waterholes)	Valeix, Loveridge & Macdonald 2012
Mara	<i>Dolichotis patagonum</i>	Argentina	Field study	GS correlated with H and PR	Taber & Macdonald 1992
Mule deer	<i>Odocoileus hemionus</i>	USA (California)	Field study	HR correlated with PD	Kie <i>et al.</i> 2002
Raccoons	<i>Procyon lotor</i>	Missouri, USA	Field experiment	HR overlap increased when clumped food resources provided (effective GS increased with PR)	Wehtje & Gompper 2011
Red fox	<i>Vulpes vulpes</i>	UK	Field study	TS partially correlated with PD; GS partially correlated with PR	Baker <i>et al.</i> 2004
Red fox	<i>Vulpes vulpes</i>	Israel	Natural experiment	Increased home ranges and decreased survival when human food sources reduced	Bino <i>et al.</i> 2010
Red fox	<i>Vulpes vulpes</i>	Tunisia (Djerba)	Field study	TS correlated with PD	Dell'Arte & Leonardi 2005
Red fox	<i>Vulpes vulpes</i>	UK (Oxford)	Field study	Groups associated with heterogeneous food sources	Doncaster & Macdonald 1997
Red fox	<i>Vulpes vulpes</i>	UK	Field study	TS unrelated to GS; PR associated with small TS and large GS	Macdonald 1983
Red fox	<i>Vulpes vulpes</i>	Israel	Field study	General invocation of RDH	Macdonald 1987
Red fox	<i>Vulpes vulpes</i>	Saudi Arabia	Field study	General invocation of RDH	Macdonald <i>et al.</i> 1999
Red fox	<i>Vulpes vulpes</i>	Switzerland	Field study	General invocation of RDH	Meia & Weber 1996
Red fox	<i>Vulpes vulpes</i>	Round Island, North Atlantic	Field study	GS correlated with PR	Zabel & Taggart 1989
Roe deer	<i>Capreolus capreolus</i>	Norway	Field study	HR correlated with PD	Mysterud 1998
Salmon	<i>Salmo salar</i>	Scotland	Lab experiment	HR correlated with PD	Valdimarsson & Metcalfe 2001
Silver-backed jackal	<i>Canis mesomelas</i>	East Africa	Field study	TS unrelated to GS	Macdonald 1983
Spotted hyaena	<i>Crocuta crocuta</i>	Tanzania	Field study	TS correlated with PD	Kruuk & Macdonald 1985
Striped hyaena	<i>Hyaena hyaena</i>	Kenya	Field study	Unusual reverse prediction: Given low H, individuals are solitary	Wagner, Frank & Creel 2008
Swamp wallabies	<i>Wallabia bicolor</i>	Australia	Field study	*HR decrease with greater H of food (authors miss that RDH can apply to multiple resources)	Di Stefano <i>et al.</i> 2011
White-nosed coatis	<i>Nasua narica</i>	Panama (Barro Colorado island)	Field study	GS related to patchy resources, but in interaction with sex	Gompper 1996
White-nosed coatis	<i>Nasua narica</i>	Mexico	Field study	HR related to PD (of waterholes), and H related to GS	Valenzuela & Macdonald 2002
White-throated magpie jay	<i>Calocitta formosa</i>	Costa Rica	Field study	TS correlated with PD; GS correlated with PR	Langen & Vehrencamp 1998
Willow tits	<i>Parus montanus</i>	Finland	Natural experiment	HR increase but no GS increase following habitat loss	Siffczyk <i>et al.</i> 2003
Wolverines	<i>Gulo gulo</i>	Northern Norway and Sweden	Field study	Female HR correlated with PD, and male HR follows female dispersion	Vangen <i>et al.</i> 2001

Asterisked findings (*) are those in which RDH predictions were not supported.
 GS, group size; H, heterogeneity; HR, home range; PD, patch dispersion; PR, patch richness; TS, territory size.

type II error. While data were often consistent with RDH, as we pointed out earlier, many other sources of variation are likely to influence territory size and group size, and without manipulation experiments, it is hard to provide conclusive support. In the following sections, we describe key empirical evidence for and against the RDH, first from field experiments and, second, from correlational studies (summarized in Table 4).

Field experiments

Conclusive tests of RDH will come from experiment rather than correlation, and field experiments are slowly accumulating. The value of opportunistic or experimental removal studies to test assumptions and predictions of hypotheses about the formation of territoriality in many species, including the badger, has long been recognized (Beletsky & Orians, 1987; Roper & Lups, 1993; Stamps, 1994). A prediction of the RDH (see Kruuk & Macdonald, 1985), and one that bovine tuberculosis control policy has unintentionally tested for us (Tuytens *et al.*, 2000), is that should a badger group cease to exist (because of removal/culling) then while the surrounding groups may readjust their boundaries they would not, as contractionists, make a long-term land grab. By the same token, should only a proportion of residents in a group be culled/removed, effectively reducing group membership, this will not alter the remaining individuals' need to exploit the same dispersion of resources as before, thus the prediction is that territory area will not contract. Monitoring the efficacy of badger removal operations at six groups central to a badger population in North Nibley (Gloucestershire), Tuytens *et al.* (2000) found that half of the neighbouring groups enlarged their ranges post-removal to include parts of the cleared area, while the remainder did not. Most ranges reverted back to their pre-removal sizes after 3 years (though not necessarily the same configurations), so the RDH was not critically challenged because it allows for badgers to reconfigure their ranges due to the availability of vacated patches, as long as they do not strive for long-term expansion.

Wehtje & Gompper (2011) compared home-range size, two-dimensional overlap and volume of intersection (VI) values between 22 raccoons with access to a clumped food resource and 19 raccoons, at an adjacent control site, that received an identical quantity of food but spread out in multiple locations. No sex differences in home-range size occurred within either food site, nor did differences in home-range size occur between the two sites. The experimental site animals, however, exhibited two-dimensional home-range overlap values and VI scores that were nearly twice those of raccoons inhabiting the control site, supporting their prediction that home ranges would overlap more where 'a clumped resource would facilitate more than one individual using a locality without incurring costs to other individuals' (p. 26). These differences were driven by increased overlap among females from the experimental site, as males from both sites had similar home-range overlap and VI scores. They concluded that the distribution of resources significantly changed the extent of spatial overlap among individuals, even though the mean home-range size within the

population did not change. Further, while overall resource availability influenced population size, the spatial clumping of resources facilitated the formation of local aggregations.

Bino *et al.* (2010) capitalized on a natural experiment when studying foxes in the face of a drastic reduction in the availability of anthropogenic food sources. The result was a rapid and distinct increase in home-range size – in one village, foxes exposed to reduced resource availability more than doubled their home-range size, and the survival rates of individuals in the treated areas were drastically reduced. They concluded that the results offer support to the RDH regarding both home-range size and density (suggested by the sharp decrease in survival) as a function of the spatial and temporal dispersion of resources. In another study based on habitat loss, Siffczyk *et al.* (2003) invoke RDH to explain why willow tits, *Parus montanus*, responded to habitat loss by enlarging their home ranges but not by reducing group size. They conclude that large home ranges incorporate as many good quality resource patches as smaller ones.

Davies & Hartley (1996) studied dunnocks at feeding sites. Where food was provided each day, dunnocks defended small, exclusive territories. At variable feeders, where food was allocated at random each day to one of several adjacent sites, dunnocks adopted larger, more overlapping ranges. In the variable feeder treatment, there was sufficient food per patch for several individuals to feed there. The territory overlap promoted by the variable feeders was not only much greater than that in the regular feeder treatment but also greater than that ever recorded under natural conditions during a 10-year study. Davies and Hartley concluded that the experiment therefore provided support for the idea that food patchiness can promote territory overlap and group formation.

The alpine accentor, *Prunella collaris*, is a territorial and polygynandrous species, with the breeding unit a group consisting of about seven members which share a group territory. Each female holds a small territory around her own nest within the larger group territory. Nakamura (1995) provided supplemental food in the form of millet seed in one or two artificial patches 200 m apart for a total of 23 group territories. The results were equivocal in terms of RDH because although groups provided with feeders did not form smaller territories than those without feeders, nonetheless, provision of extra food did result in an increase of group size (with no change in the sex ratio). The increase in group size without a contraction in territory size is in accord with RDH predictions. However, this raises the question of why the one or two additional patches did not lead to territory shrinkage, assuming the accentors are contractionists. The answer might lie in the placement of the supplemental patches, the timing of their arrival relative to the process of territorial establishment and the time over which accentors assess patch dispersion: in a seasonally or inter-annually variable environment, territorial configuration might adapt only over long periods (as in the constant territory size hypothesis).

Extending the taxonomic range beyond vertebrates, Tanner & Jackson (2012) observed that non-social European shore crabs formed groups in response to resources becoming clumped. In a lab experiment, exploratory individuals aggre-

gated into cohesive, stable subgroups (moving together even when not foraging), but only in tanks where resources were clumped. No such non-foraging subgroups formed in environments where food was evenly dispersed.

Correlational studies

Many field studies have evoked RDH when exploring the link between patch dispersion and territory size, and patch richness and group size. While such correlations are less conclusive than the experimental studies above, the replicability, taxonomic range and diversity of applications is remarkable.

Does territory size predict group size?

First, a weak prediction. If patch dispersion determines territory size, and patch richness determines group size, then this implies that territory size and group size can be independent – giving a further prediction of the RDH in environments where resources are patchy (see Macdonald, 1983; Johnson *et al.*, 2002b). If, by contrast and among other possibilities, resources are uniform, then the null expectation is that territory size must increase with group size because more bodies demand more food (or other resource). A lack of correlation, therefore, can at least be a signal that resources are not uniform and something else is going on – it can be a useful first check.

In this section, however, we focus on studies that specifically test the patch dispersion and richness predictions, for two reasons: (1) a lack of correlation between territory size and group size is a weak prediction (a lack of correlation may result from type II error or any number of unmeasured, confounding or interacting factors); and (2) whether there is a correlation or not, RDH may still be in play (patch dispersion and richness may affect group size and territory size over and above any dependence they do show). As explained previously (Johnson *et al.*, 2002b), one must go on to test additional independent variables of the hypothesis, and only in combination with other predictions would a group size–territory size relationship provide evidence for or against RDH.

A specific example illustrates the point. Robertson *et al.* (2014) published an analysis based on the group sizes of badgers in 43 territories studied between 1981 and 2010, which revealed a weak correlation between territory size and group size (in their main model, $R^2 = 0.15$; particularly driven by the numbers of adult males in the group), at odds with analyses of the rather similar badger population at Wytham (e.g. Johnson *et al.*, 2001). Notwithstanding the weak correlation, the caveats outlined above, and no data on whether resources in the study site are patchy, this was interpreted as a rejection of RDH.

As the authors themselves point out, the large amount of variance unexplained by the correlation between group and territory size leaves abundant room for factors such as resource dispersion to be at play. If X and Y are not correlated, they must depend on other factors; if X and Y are only weakly related, they must still depend to a large extent on other factors. Since there were no measures of resource dis-

persion or richness, it is not possible to conclude whether these critical variables affected group sizes and territory sizes or not.

Before moving on to more explicit studies of these variables, note that of course the RDH does not assume resources are always or everywhere patchy (though that might often be the case). Rather, the RDH suggests that where resources are patchy in the environment, group size and territory size need not correlate (and instead depend on the richness and dispersion of resources). Where resources are not patchy, or not patchy enough, then the RDH itself also predicts a correlation between group size and territory size (to clarify this: if heterogeneity is low enough in Fig. 1, there is no room for secondaries and animals would instead have to scale territory size with group size). It is therefore perfectly conceivable that in many study sites, resources are not patchy, which is why it is vital that researchers attempt to measure, not surprisingly, resource dispersion in studies of the resource dispersion hypothesis! We cannot test theories only by measuring their dependent variables.

So while the RDH was partly motivated to explain empirical puzzles in which territory size did not scale up (as one would otherwise expect) with group size, much more important for RDH are tests of stronger predictions derived from the model: (1) whether patch dispersion predicts territory size; and (2) whether patch richness predicts group size. We detail studies of each of these predictions in the sections below.

Does patch dispersion predict territory size?

Food resources

RDH thinking was anticipated by Rowe-Rowe (1977) when he suggested that sociality in otters may have arisen almost by default, there being no selective pressures against group foraging, particularly on crabs or in muddy rivers in the tropics. Because some fish shoal, they form patches that vary both in time and space; piscivores are therefore promising candidates for illuminating RDH (see also Schneider & Piatt, 1986). Among the coastal otters of Scotland, solitary males fish diurnally, occupying 2.7–4.5 km territories (within 100 m of fresh water for bathing), overlapping several groups of 2–5 territorial female otters, of which several or all bred each summer (Kruuk & Hewson, 1978; Kruuk *et al.*, 1989). The members of these spatial groups operated separately (spending more than half their time in individual core areas), with the female groups configured around fresh water and rich fishing patches, which in RDH terms were both not easily partitioned but shareable. Similar mechanisms might explain the socioecology of Cape clawless otter, among which total home-range length correlated with mean reed bed (a high-density food patch) nearest neighbour distance (Somers & Nel, 2004), and groups of up to four female hairy-nosed otters in Cambodia (Otter, 2003; Hwang & Larivière, 2005).

Shoals of fish have similar attributes to swarms of insects. One of the seminal studies at the roots of RDH was Bradbury & Vehrencamp's (1976a,b) description of neotropical bats, whose territory sizes were determined by the dispersion of insect swarms over rivers, whereas their flock sizes were

determined by the richness of these swarms. Bats have continued to be a rich source of evidence for RDH, and Nicholls & Racey (2006) drew attention to the contrasting socio-spatial system of two morphologically indistinguishable species of pipistrelle bat. The home ranges of *Pipistrellus pipistrellus* were three times the size of those of *P. pygmaeus* (with huge extra energetic costs). Furthermore, the *P. pygmaeus* colony was approximately 2.5 times larger than the *P. pipistrellus* colony. The authors concluded it was plausible that the dramatic difference in range size between these morphologically similar and sympatric species was due to the difference in the spatial dispersion of suitable foraging patches.

Returning to badgers, Kruuk & Parish (1982) demonstrated that, across Britain, when worm-rich habitat patches were more spread out, badger territory size was greater. Further corroboration was to come from the work by Da Silva *et al.* (1993) in Wytham Woods. Here, the conversion of earthworm-poor arable land to earthworm-rich pasture resulted in an effective reduction in food patch dispersion, over a 15-year period. Mean territory size among the resident badger groups affected underwent a corresponding decrease from 0.9 km² in 1974 to 0.3 km² in 1987, with associated changes in territorial configurations.

Studying badgers living in the predominantly coniferous habitat of upland north-east England, Palphramand, Newton-Cross & White (2007) also found significant positive correlations between territory size and the number of grassland patches, but negative correlations with the proportion of grassland, concluding that this was consistent with RDH. They also reported that seasonal home ranges of individual badgers were largest in autumn, followed by summer and spring, then winter; a pattern likely reflecting seasonal changes in food availability within the area, and not readily interpreted as responses to reproductive cycles. Research from low-density badger populations in Portugal (Rosalino, Macdonald & Santos-Reis, 2004), Japan (Kaneko *et al.*, 2014) and south-west Spain (Rodriguez, Martin & Delibes, 1996), reveals that where fruit, cereals, invertebrates, amphibians and mammals contribute more towards primary food resources than do earthworms, less gregarious social systems arise, and home-range sizes are larger where food patches are more dispersed.

Revilla & Palomares (2002) describe interesting social dynamics among badgers in the Donana region of south-western Spain, which they conclude do not support RDH. In winter and spring, when rabbits were most available, dominant females and subordinates used only a small fraction of their territories, moved short distances, slowly covering small areas each night. In summer, when food availability was lowest and badger body condition poor, dominant females were the only individuals using all the territory available. Food availability increased again in autumn, as did body condition, while range sizes were again reduced. Dominant males used the same proportion of their territories over all seasons. However, in winter (reproductive season), they moved faster, over longer distances, and covered larger areas per period of activity. Revilla and Palomares (*op. cit.*) conclude that space use by dominant males was affected by

different factors from that of dominant females and subordinates. They further listed three reasons why RDH fell short as an explanation of group living in their populations: (1) territoriality in each pair of primary animals was driven by different factors (trophic resources for females and males for males); (2) dominant males acted as expansionists; and (3) territory size was related to its richness and not to patch dispersion. They therefore propose an integrative hypothesis to explain not only group formation but also interpopulation variability in the social organization of badgers within ecological, demographic and behavioural constraints and in the light of theory on delayed dispersal. In fact, much of the system described by Revilla and Palomares actually accords with RDH. Where prey availability varies periodically, the temporal version of RDH predicts that the territory will be configured to accommodate the troughs in food availability (Carr & Macdonald, 1986). In the case of Revilla's and Palomares' badgers, this seasonal trough appears to be in summer. The notion that the spatial arrangements of females are driven by food, and those of males by females is well-established in evolutionary biology (Emlen & Oring, 1977; Lukas & Clutton-Brock, 2013) and not at odds with RDH (see earlier discussion of mating systems).

Early support for RDH came from the Arctic foxes studied by Hersteinsson & Macdonald (1982) that survived by beachcombing on the fjords of north-west Iceland. Using driftwood as a proxy for the pattern with which food was washed ashore, they found, as predicted, that territory lengths were determined by the distance between bays in which flotsam and jetsam were washed up, whereas group size was related to the amount of food washed up. Eide, Jepsen & Prestrud (2004) documented the summer home ranges of Arctic foxes, and found that small home ranges with large overlap were characteristic for coastal areas where prey was concentrated in small patches and predictable both in space and time. Medium home ranges and some overlap occurred inland where prey was clumped in larger patches and less predictable. Large home ranges with little overlap occurred inland where prey was widely scattered and unpredictable. They concluded that the spatial dispersion and richness of prey resources explained most of the variation in Arctic fox spatial organization and that the RDH framework could be used to explain the presence of relaxed territoriality found in their study.

Several other field studies of canid societies prompt explanations compatible with RDH. For example, Geffen *et al.* (1992) found that for Blandford's fox in a desert environment, the variance in home-range size was explained by the mean distance between the main denning area and the most frequently used patches of creekbed, the crucial habitat for foraging for insects. In a seasonally flooded environment, Macdonald & Courtenay (1996) suggested that the territory size of crab-eating foxes, *Cerdocyon thous*, was determined by the dispersion of dry land at the peak of the flooding, and speculated that groups were facilitated because these dry patches required by a pair could support several secondary group members. Studying coyotes in a tropical deciduous forest in Jalisco Mexico, Hidalgo-Mihart *et al.* (2004) compared animals using a landfill dump, where food was available

throughout the year, and animals with no access to this clumped resource, where food was distributed between widely spread patches whose dispersion varied seasonally. Home ranges of coyotes around the landfill varied from 0.9 to 9.5 km², whereas those away from this anthropogenic food source varied from 10.9 to 43.7 km². Further, the coyotes around the landfill formed a spatial group of four adults, whereas elsewhere they lived as pairs. The authors concluded that under the circumstances of their study, coyotes followed the postulates proposed by the RDH.

In what is essentially an exploration of the pressures for expansionism (greater collective strength for intraspecific hostility) over and above the facilitating effect on group living of large, sharable prey, Spong (2002) studied the home range and group sizes of lions in Tanzania, and asked whether space use is related to pride size, habitat or relatedness. Home ranges varied in size, but size showed no correlation to number of adult females in the pride or to habitat type, and territory sizes were not obviously affected by group size or type of habitat within the home range. Spong concluded that space use within-home ranges seems to be driven mostly by prey availability. Extending these findings, Hayward *et al.* (2009) used relationships between prey abundance and predator space use to create equations to predict the home-range size of lions and leopards, and concluded that prey abundance is the key factor in determining space use of large predators. Referring to the RDH, they concluded that the dispersion of prey was the primary factor determining home-range size in lions and leopards. Perhaps the strongest support for RDH in lions, which Macdonald first proposed in 1983 having re-plotted Schaller's 1972 data, concerns the function of waterholes, and specifically, the prey that concentrates around them in the dry season. In Hwange National Park, Zimbabwe, Valeix, Loveridge & Macdonald (2012) found that the distance between two neighbouring waterholes was a strong and significant determinant of lion home-range size, providing strong support for the RDH prediction that territory size increases as resource patches are more dispersed in the landscape.

Of course, RDH is concerned with available resources, which competitors may interfere with, and the study of African wild dogs, *Lycaon pictus*, by Mills & Gorman (1997) is among those to illustrate the constraints on availability imposed by intra-guild hostility. They point to the apparent paradox that the dogs exist at their lowest density where their food is most abundant, because they are dodging lions. Mills and Gorman (op. cit.) argued that RDH falls short in these circumstances insofar as the pattern of food dispersion does not adequately explain the distribution and densities of dogs, amidst the complications of predation by, and competition with, other carnivores. However, the RDH is concerned with food that is available (i.e. given any competition), and the dispersion of these resources after the landscape of fear and risk (e.g. Valeix *et al.*, 2009), because of the presence of lions, has been accounted for. This renders an area, and the prey therein, less available to wild dogs in a way no different to the effect of, for example, dense vegetation, thus redrawing the map of food availability.

In Macdonald *et al.*'s (2007) tale of two cavies, RDH is also applied to Taber & Macdonald's (1992) work on maras radio-tracked in Patagonia. They travelled as monogamous pairs that bred either alone at solitary burrows or communally at settlements where up to 29 pairs shared warrens. Two, non-exclusive hypotheses might explain the adaptive significance of these settlements: one relates to predation (through the protective influence of human dwellings), but the other relates to resource availability (through the indirect effect of ground water and sheep dung on vegetation). Maras face extremes of resource dispersion between the wet and dry seasons: in the former, sparsely dispersed grazing and interference competition favour spacing out and territoriality; in the latter, clumping of resources facilitates pairs congregating in herds around outstations and dry lagoons. Superimposed upon the ecological factors favouring spacing out during the wet season are the sociological factors that cause the maras to den communally. The resulting compromise is a social system unique among mammals.

Marable *et al.* (2012) found that home ranges of eastern wild turkeys were greater in a more fragmented site than in a less fragmented site, which they concluded supported the RDH. Moreover, home-range sizes were related positively to within-home range variability in vegetative greenness measured by the normalized difference vegetation index.

Using field data from swamp wallabys, Di Stefano *et al.* (2011) report that home-range size decreases with resource heterogeneity, in terms of the spatio-temporal distribution of multiple resources. Because they interpreted RDH in terms solely of food resources, they judged it inadequate in the context of the wallabies' dependence on diverse resources. However, RDH embraces multiple resources (not just food, but water, dens etc., as per Table 2), so the authors' interpretation of wallaby spatial organization in terms of a multidimensional resource surface (rather than 'with simple additive or interactive effects of separate resources') can be seen to fit with RDH.

Finally, the RDH sheds light on (and the differences between) our two closest living relatives, chimpanzees *Pan troglodytes* and bonobos *P. paniscus*. Because of their importance as models for human origins, much attention has been directed towards understanding their ecological and behavioural differences. Many primatologists have come to the conclusion that these interspecific differences are 'at least partially [due] to differences in food patch size and distribution and to bonobo use of herbaceous groundcover plant foods in addition to fruit' (Stanford, 1998, p. 402). Bonobos' range in rainforested areas to the south of the Congo river, while chimpanzees occupy more diverse habitats spanning West to East Africa. Bonobos tend to forage in larger groups than chimps, and this appears to be possible because they feed on widely available terrestrial herbaceous vegetation (this has formerly been called the 'THV hypothesis'; Wrangham, 1986; Wrangham, Gittleman & Chapman, 1993; Chapman, White & Wrangham, 1994). By contrast, chimps rely much more heavily on fruiting trees. Even when fruits are scarce, chimps continue to search for them every day. Notably, fruiting trees

in tropical forests are clumped resources (one tree ripens among many that do not), but rich when available. This leads to chimpanzee communities splintering into subgroups of varying size, depending on food availability. Empirical studies have shown that ‘Group size in chimpanzees rapidly adjusts to monthly changes in the density and distribution of fruiting trees’ (Wrangham, 2009, p. 129). This fundamental difference in feeding ecology has major knock on effects for the rest of the two species’ behavioural ecology, including sex differences in foraging, mating patterns, coalition formation, and intra- and inter-group aggression. Key differences between chimpanzee and bonobo social behaviour, therefore – a subject of long-standing and intense debate – may have their origins in the RDH.

Water as a resource

Up to now we have focused on food as the critical resource. Another critical resource for many species that is also dispersed, and varies in patch richness, is water. Comparing areas in which dry season waterholes were less, or more, widely dispersed, Valenzuela & Macdonald (2002) found that the average seasonal home-range sizes, which varied between 45 and 352 ha, of white-nosed coatis in Mexican tropical dry forests were determined by the dispersion of water sources during the dry season (although they did not establish what determined group sizes).

Herrera & Macdonald (1989) observed that capybaras depend upon access to permanent surface water, but also, during periods of flooding, they need dry land. Where there is such water, their territories are configured to encompass sufficient resources to ensure survival under widely different seasonal conditions. At the height of the wet season, when dry sanctuaries were vital, each capybara needs sufficient ‘banco’ (elevated) habitat to survive, but these islands may also support additional group members. Similarly, in the parched environment of the dry season, each capybara needs access to ponds. It may be that a territory sufficiently large to encompass widely spaced ponds in the dry season automatically encompassed additional banco for the wet season. In this case, the dispersion of one (or two) critical resources in one season would be correlated with the richness of the third critical resource (in this case, the bottleneck) in the other season. The observation that larger territories are apparently configured to embrace two ponds, and thereby acquire additional intervening banco, is compatible with this suggestion.

If water, when available, is not limiting (e.g. a large lake, or a year-round river), we may also expect an impact on the behaviour of those using it and the absence of competitive exclusion. In his introduction to Robert Ardrey’s *Territorial Imperative*, Irven DeVore noted that, in the dry season, usually hostile baboon groups at a single scarce waterhole do not fight (Ardrey, 1966, p. xv). Indeed, in the study mentioned above, several groups of capybaras could be observed to meet and mingle, and then part, around large lagoons in the dry season. Such scenarios may extend to humans. In

The Alchemist, Paul Coelho describes an ancient code in the North African desert that, during war time, an oasis is neutral territory (Coelho, 1988). Anthropological studies have similarly noted that, ‘where resource patches are dispersed but non-depleting (e.g. dry season waterholes) communities might be forced into periods of coexistence’ (Moore, 1996). However, waterholes may not always be sharable enough, if they are small or liable to exhaustion (e.g. dry season ponds, small springs), and certainly, there are documented cases of conflict rather than coexistence, such as the Walbiri hunter-gatherers of Australia who ‘fought a neighbouring group for possession of a water hole’ (Keeley, 1996, pp. 115–16). The sharability of life sustaining water sources may make the difference between war and peace.

This contrast between limited and mega-rich patches such as large or replenishing waterholes suggests something else interesting about the logic of RDH. The availability of dispersed patches may be able to support larger individual animals, as well as larger groups of animals – in either case, a larger biomass is sustained. This idea is starkly illustrated by the question of how some species became so large. One puzzle has been how massive sauropod dinosaurs (the giant long necked species such as diplodocus, brachiosaurus and brontosaurus) were able to survive in the lowland floodplain basin in present-day south-west US (the Morrison depositional basin). These environments were subject to seasonal dry climates that were unlikely to be able to support the water and nutritional needs of such massive creatures – the largest land animals of all time – and hence ‘the common occurrence of sauropods in this basin has remained a paradox’ (Fricke, Henceroth & Hoerner, 2011, p. 515). Oxygen isotopes in tooth enamel now suggest that, in contrast to earlier ideas that they could barely move, these megaherbivores ranged to volcanic highland water sources several hundred kilometres away (which provided both water and associated food). In short, it appears that ranges had to expand to include critical resources – and these patches, when available, could sustain many individuals. But here, the additional remarkable insight is that these resources could sustain the biomass of massive individual animals as well as (or instead of) the biomass of multiple individuals. Where resources are rich patches therefore, RDH may facilitate not only the evolution of sociality, but also the evolution of gigantism (‘secondary’ food security can represent more body mass, not more animals; Table 5). Indeed, this suggests that environments that are more heterogeneous, have richer patches, or faster renewal, may foster the evolution of larger species. Bergmann’s rule, the tendency for animals to have larger body sizes in colder climates, is traditionally explained as an adaptation to the greater demands of thermoregulation or reduced competition at high latitudes. A novel explanation we suggest here is that it might also be a consequence of more patchy resources or greater patch richness. McNab (1971) argued that the thermoregulation account does not hold up, and the rule is more likely to be due to latitudinal changes in the distribution of prey, or of competitors – in short, a possible influence of RDH.

Dens as a resource

Doncaster & Woodroffe (1993) proposed that another resource dictating the size and shape of badger territories, which could potentially also constrain local population density, might be the limited availability of suitable sett sites (see also Blackwell & Macdonald, 2000). However, Macdonald *et al.* (2004b) found that, in Wytham, new sett sites appear to have been readily available since the trapping regime began (in 1987), accommodating increasing population size (Macdonald & Newman, 2002; Macdonald *et al.*, 2009). These new setts were not measurably inferior to established ones (in terms of the weight or reproductive success of residents), thus sett site limitation does not seem to have been a limiting factor in social configurations (Blackwell & Macdonald, 2000).

Setts have, however, been found to be limiting in some low-density badger population areas in Mediterranean habitat (e.g. Loureiro *et al.*, 2007). In Mediterranean cork oak woodlands in south-west Portugal (Rosalino, Macdonald & Santos-Reis, 2005), the main factor limiting badger density is the availability of suitable sites for setts. Similarly, Molina-Vacas *et al.* (2009) concluded that sett dispersion was the critical determinant of badgers in Mediterranean Spain. In central China, Zhang *et al.* (2010) reported that the scarcity of suitable sett sites appeared to be a limiting resource for the population of ferret badgers, potentially underlying the population's observed socio-spatial gregariousness, and delimiting the size of individual home ranges.

Females as a resource

The procyonid white-nosed coati is unique within the order Carnivora in maintaining a dichotomous social structure of group living (cooperative and closely related) females and solitary males (Gompper, 1996; Gompper, Gittleman & Wayne, 1997). Groups (called bands) comprise from 6 to over 30 related and unrelated females and their immature offspring (Gompper *et al.*, 1997; Gompper, Gittleman & Wayne, 1998). All adult males remain solitary with the exception of a brief (approximately 2-week) synchronous breeding season. On Barro Colorado, Panama, Gompper (1996) showed that reliance on patchy, shareable frugivorous/insectivorous food resources interacted with sexual dimorphism to affect social organization. It appears that female coalitions achieve superior access to patchy resources that are otherwise unavailable because of small body size relative to competing males. In contrast, larger males are able to access food patches without living in groups, which might increase foraging competition.

Vangen *et al.* (2001) cite RDH in concluding that the spacing of female wolverines is determined by the abundance and dispersion of food, whereas the distribution of males is determined by the distribution of females, at least in the breeding season. They conclude that, in keeping with RDH, juveniles and subadults can be incorporated into their parents' home in years with good prey availability (echoing the inter-annual emphasis of von Schantz, 1984b).

In line with the generality of sex differences proposed by Emlen & Oring (1977), Kaneko *et al.* (2014) found that in a

population of Japanese badgers (*Meles anakuma*) living at a density of 4 individuals per km², the average home-range size of males expanded in the mating season, and was significantly larger than the more consistent range size of females. Females with cubs had home ranges exclusive of other adult females, configured around areas rich in food resources, indicative of intra-sex territoriality. This exemplifies how the constant territory size hypothesis (CTSH; von Schantz, 1984a,b,c), interacts with the RDH; recall that the CTSH identifies an 'obstinate strategy' – evidenced if individuals adopt a territory size adjusted to its needs during low resource availability periods – and a 'flexible strategy', where territory size varies seasonally with resources (e.g. access to females for males).

Does patch richness predict group size?

The prediction that territory size will be determined by patch dispersion becomes especially important to RDH in combination with the less intuitive prediction that territory size and group size may sometimes be unrelated, the latter being determined by resource richness, heterogeneity and renewal. It is therefore disappointing that there has been little advance in empirical evidence on the corollaries of group size among studies of badger group size in the last decade. Across Europe, controlling for latitude, Johnson *et al.* (2002a) demonstrated that badger group sizes are large only where territories are small. Assuming similar body masses and energetic costs, only superior local resource richness (or renewal) can permit this (and patchy resources are also implicated because if they were uniform, individual or pairs of badgers could divide up the landscape into territories of their own; instead, they share). Furthermore, in 1987, Kruuk & Parish (1987) reported that, in a Scottish population, as worm biomass decreased over a 5-year period, there was a decrease in the mean number of badgers per clan (albeit statistically non-significant); however, because this occurred without any change in patch dispersion, there was no significant change in clan territory area (although individual home ranges increased). Da Silva *et al.* (1993) found that, while group size was unrelated to territory size, the number of cubs born per territory, and the number of breeding females therein, did increase with the proportion of territory composed by deciduous woodland (an important foraging habitat), as did the average body weight of male badgers.

At an extreme of sociality, giant otters of Manu National Park in Peru live in groups varying between a pair and extended families of up to 13 individuals, each of which includes only a single breeding male (Groenendik *et al.*, submitted). These feed on fish that are particularly numerous in oxbow lakes, with only two species of fish comprising over 70% of the diet. The population segregated into 12 territories, and each encompassed one or more lakes together with the associated river and swamp. Territories overlapped, but their cores (the lakes) were exclusive and almost certainly defended. Larger groups occurred in territories with larger cores, and pairs in territories with larger cores, and thus larger groups, produced more cubs annually. Further, in years when a territory had more non-breeding helpers, the cubs born that year

were more likely to survive to be yearlings, and cubs produced on richer territories were more likely to disperse successfully. In short, more cubs were produced in territories with richer patches, and those cubs were 'fitter'.

Although the basic social unit of many canids, especially vulpine ones, is spatial monogamy, almost all those that have been studied at least occasionally incorporate secondary group members (Macdonald, Creel & Mills, 2004a). Explaining the adaptive significance of these small spatial groups among red foxes was among the stimuli for early versions of RDH, where rich food patches in suburban gardens were associated with relatively tiny territories occupied by groups of up to five adults (Macdonald, 1981, 1983). Under the different spatial circumstances of drifting territoriality, Doncaster & Macdonald (1997) also interpreted the group formation of Oxford City's urban foxes, perturbed by relatively high mortality on the roads, in terms of temporally and spatially heterogeneous foods: their diet comprising largely of scavenge (37% dry weight), followed by earthworms (27%) and small mammals (16%; Macdonald *et al.*, in press). On Round Island in the north Atlantic, Zabel & Taggart (1989) invoked RDH to explain why red fox group sizes became smaller as seabirds became less abundant, and the number of reproductive females per group also declined.

The same principle applies to temporal variation even in homogeneously dispersed resources. For example, red foxes depending on a cyclic vole population might configure their territories to sustain them through trough years, and accommodate extra group members in peak years (von Schantz, 1984b; Lindstrom, 1993). Moehlman (1989) invoked a similar argument to explain variation in group size within constant territory sizes in golden jackals, and a similar temporal emphasis of RDH might apply to kit foxes or bat-eared foxes adapting their territories to periods of drought (Egoscue, 1975; White, Vanderbilt & Ralls, 1996; Maas & Macdonald, 2004) or crab-eating foxes adapting theirs to periods of flooding (Macdonald & Courtenay, 1996).

Considering the patches of habitat that supported a high availability of rodent prey for Ethiopian wolves, *Canis simensis*, Tallents *et al.* (2012) found that the number of subordinate adult females and yearlings in each pack was correlated with the abundance and spatial predictability of foraging habitats and prey. This matches the prediction of the RDH that the number of secondary animals in a group will be determined by resource richness. The Ethiopian wolf study encompassed two areas: at Tullu Deemtu, patches of good habitat were widely spaced and territories averaged 10.5 km², whereas at Web and Sanetti, good habitat patches were less widely dispersed and territories averaged 4.4 km² (Marino *et al.*, 2012). As predicted, large and small territories both contained similar areas of rich habitat, but contrary to prediction, despite the similar amount of rich areas, group sizes in Tullu Deemtu were smaller (mean group size 2.4) than those in Web and Sanetti (mean group size 6.4). The authors speculated that this was because the actual rodent abundance in rich habitat patches at Web and Sanetti was higher than those in the rain shadow of Tullu Deemtu.

Newsome *et al.* (2013), studying dingoes, concluded that larger groups of dingoes associated with areas of abundant food supported RDH, as did variation in home-range size, which was determined by the dispersion of food patches. However, with an argument that loosely parallels the observations of Wilson & Shivik (2011) for coyotes around rich food patches, Newsome *et al.* (2013) conclude that the predictive power of RDH is weakened where super-abundant food is available and dingoes from far afield make excursions to usurp the territory boundaries of those defending the rich food sources. Indeed, a not dissimilar situation applied to golden jackals in Israel, where one large group defended a rich food patch, from which neighbouring animals pilfered (Macdonald, 1979). A key point here is that RDH does not aspire to explain every nuance of social organization, and the fact that it cannot accommodate all confounding factors or intricate ecological factors is not a failure of the hypothesis.

Another type of very rich patch comes in the form of the large ungulate prey of big cats. Foraging group size might be affected by the body mass of prey (analogous to the richness of a food patch) as distinct from their abundance. One female lion, weighing approximately 141 kg, can generally monopolize carcasses of less than 100 kg, but is unlikely to keep other females at bay from larger carcasses (Packer, 1986). Schaller (1972) reported that when seven lionesses in a pride fed mainly on wildebeest (mean 122.3 kg), an average of 6.4 of them ate together, whereas when they killed Thomson's gazelle (13.3 kg), only 3.6 fed together. When zebra (226.7 kg) moved into one pride's range, Schaller saw feeding groups of seven lionesses eating together. These observations suggest that another key factor in group formation is the abundance of accessible large prey (Liberg *et al.*, 2000; a point which we argue below might have affected the evolution of human society).

As mentioned above, for the lions of Hwange National Park, waterholes are a powerful proxy for prey availability, and the dispersion of waterholes determines territory size. Additionally, the mean number of herbivore herds using a waterhole, a good proxy of patch richness, determined the maximum lion group biomass an area could support (Valeix *et al.*, 2012).

Procyonid kinkajous den communally, and for 20% of their time, fed together in groups in large fruiting trees, otherwise foraging alone in small patches of fruit (Kays & Gittleman, 1995, 2001; Kays, 1999; Kays, Gittleman & Wayne, 2000). Kays & Gittleman (2001) observed four social groups, each consisting of a single adult female, two adult males, one sub-adult and one juvenile. Among adults, males fed in groups more often than did females, and kinkajou groups were larger in larger fruiting trees.

Studying magpie-jays, Langen & Vehrencamp (1998) revealed that the amount of acacia and other food resources determined the size that groups could attain. The dispersion of two patchy habitat types, pasture and woodland, constrains where territories can form, whereas food resources, especially the fruits of bull-horn acacias, place a ceiling on the size that groups can attain. They conclude that resource dispersion may play an important role in group formation in many other

Table 5 Novel applications of RDH, helping to account for ecological phenomena beyond its traditional focus on the formation of spatial groups

Domain	Issue	RDH insight	Examples
Biogeography	Correlates of sociality	Social species more common in variable environments	Global distribution of cooperatively breeding birds (see text)
Biodiversity	Species coexistence; guild diversity	'Secondary' food security can support more species instead of more individuals	Plankton; carnivore guilds (see text)
Body size	Gigantism	'Secondary' food security can support more biomass instead of more individuals	Sauropod dinosaurs; McNab's (1971) explanation of Bergmann's Rule (see text)
Cooperation	Group hunting	Cooperation can increase the number and richness of patches	Lions, hunting dogs, chimpanzees
Synergy	One species increases access to resource patches for another species	Cooperation can increase the number and richness of patches	Honey guides and honey badgers; fish and seabird feeding frenzies
Biological invasions	New species invading already occupied territory	Invasions more likely in variable environments	See Davis (2009)
Tragedy of the commons	When are resources more likely to be shared (among humans)?	Spatio-temporal variation increases the efficacy or necessity of sharing	See Ostrom (1990)

group territorial social systems, but that the relationships remain undocumented because of inherent difficulties in measuring the relevant resources. Cortes-Avizanda *et al.* (2011) observed that Egyptian vultures and black kites aggregate more, and in larger groups, where resources were both more clumped and more abundant, while Chaves-Campos & DeWoody (2008) point out the relevance of RDH to antbirds because army ant colonies are inherently patchy over space and time, such that specialization on ants could itself promote group feeding. This brings us to a final point. Where a given prey species is patchy, any predator of that same prey species (or set of similar prey species) is likely to come under the RDH umbrella, since they face essentially the same game of dice (e.g. antbirds and anteaters). The spacing patterns of whole guilds may therefore have a common ecological basis.

Extending insights across species

RDH offers insights not only into variation within and between populations, but also variation among species (Tables 3 and 5). Scaling laws predict that metabolic needs scale as the 3/4 power of body size, and across species these metabolic needs scale with home-range size (Kleiber, 1975; Reiss, 1988; West, Brown & Enquist, 1997; the precise exponent of which has been much debated). However, plotting these relationships for the mustelids, social species often (though not always) fell below the fitted regression line, suggesting that they are able to coexist in an area smaller than one would expect on the basis of their (mean group sizes') metabolic needs alone (Johnson *et al.*, 2000). One null hypothesis is simply that key food resources for these species occur at greater density (but not greater patchiness). But if so, why should this be the case for social species more than others? Individuals could simply divide up territories into smaller plots. An alternative explanation is that social species have smaller than expected home-range sizes because they are exploiting patchy resources (yielding a greater total richness, when available, than the territories of otherwise similarly sized, non-social species). This is only correlational evidence,

but exactly the pattern we would predict if the RDH is an important facilitator of social groups.

Further evidence comes from birds. A recent study compared 45 species of African starlings, some of which breed cooperatively while others do not (Rubenstein & Lovette, 2007). The authors found that cooperative breeders tend to inhabit semi-arid savannah habitats where rainfall is highly unpredictable (as they note, 'Savanna habitats are not only highly seasonal, but also temporally variable and unpredictable', p. 1414). By contrast, non-cooperators dwelt in forests where rainfall was more stable. One might think this is a different kind of variation from that invoked in RDH – large-scale regional climate variation that is independent of resource patchiness in any individual's home-range. However, regional climate variation and unpredictability translates directly into temporal – if not spatial – variation in resources in any territory, however small. Using a phylogenetic analysis, the authors were able not only to control for the possible confound of ancestry in these behavioural patterns, but also show that cooperative breeding had independently evolved in lineages that had moved into savannah habitats. The study suggests that patchy resources may remain an important condition for sociality to persist even after cooperative behaviours have evolved. A larger follow-up study found the pattern scales up to the global level, with a comparison of 95% of the world's bird species also finding that cooperative social systems tend to be associated with more variable environments (Rubenstein, 2006; Jetz & Rubenstein, 2007). In short, variable environments predict social groups. Now, RDH does not directly predict cooperative breeding, but it does predict that large group sizes are more likely to coalesce in variable environments, laying the foundations for such behaviour to evolve.

RDH and biodiversity

The core idea of RDH is that where resources are heterogeneous, individuals' home ranges can overlap with minimal costs, resulting in spatial groups. However, extrapolation of

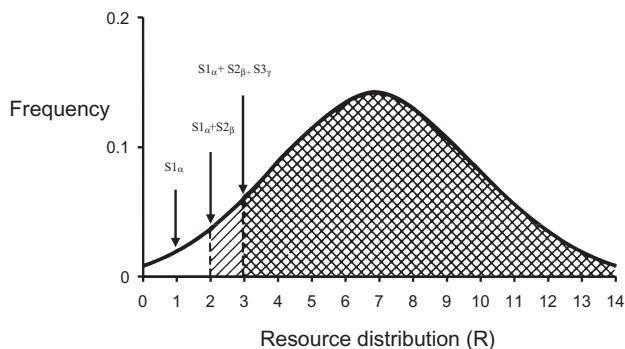


Figure 2 How resource dispersion supports biodiversity. The logic is identical to Fig. 1 for the coexistence of conspecifics, but here additional individuals are members of other species (as well as or instead of additional conspecifics). If resource patches have a certain probability of availability, then several must be simultaneously defended to guarantee some probability of finding enough food for a 'primary' resident of species 1 ($S1_\alpha$) in a given period. A frequency distribution of availability across all patches (here, arbitrarily, $n = 1-14$) indicates the proportion of feeding periods on which the total amount of resources available will exceed $S1_\alpha$. A 'secondary' – a member of another species, species 2 – can join the territory when their own resource needs ($S2_\beta$) are met on top of those of the primaries (i.e. $S1_\alpha + S2_\beta$), and a 'tertiary' – a member of a third species, species 3 – can join the territory when their resource needs ($S3_\gamma$) are met on top of the other two (i.e. $S1_\alpha + S2_\beta + S3_\gamma$). And so on. As in Fig. 1a, the area under the curve illustrates the proportion of times ['critical probabilities' (Cp)] that such conditions occur for $S2$ ($Cp_\alpha = 0.95$; upward hatching) and $S3$ ($Cp_\beta = 0.90$; downward hatching). Wherever these two distributions overlap (i.e. the cross-hatched area), all three species attain their food requirements. Changing the shape of the distribution will not alter $S1_\alpha$, $S2_\beta$ or $S3_\gamma$, but it will alter the critical probabilities associated with them, leading to a different prediction for group size. Hence, as with Fig. 1b, greater resource heterogeneity (a flatter curve but with the same total area), will increase the number of species that can coexist. One might think that not many species could be sustained in such a scenario (especially if there are also multiple individuals of each), but if resource patches are rich, or if resource needs are very different (i.e. $S1_\alpha \gg S2_\beta \gg S3_\gamma$), perhaps because the three species are elephants, dung beetles and bacteria, then many species can coexist.

this exact logic can account for coexistence among different species as well because RDH predicts reduced interspecific competition within overlapping niches – regardless of who the competitors are (Fig. 2). Niche breadth will mediate the effect: species with broader niches compete relatively less. This predicts that guilds are more biodiverse in areas where resources are more heterogeneous, in comparison to similarly rich, but more homogenous areas. Biodiversity in general has been shown to be higher on the edges of ecotones, where habitats are mixed, or in zones of flux, than within stable homogenous areas (Fjeldsa & Lovett, 1997). The idea, therefore, seems plausible.

The most striking implications come at the general level of biodiversity theory. The mechanisms underlying biodiversity are still poorly understood (Stevens, 1989; Blackburn & Gaston, 1996; Keddy & Weiher, 1999), and new insights could

have important implications. One debate has been between niche-assembly theories (Tokeshi, 1998), which focus on competition-driven specialization to different niches versus dispersal-assembly theories (Hubbell, 2001), which rely on an underlying assumption of per capita ecological neutrality between individuals of different species. RDH offers insight into how individuals sharing the same, but patchy, resources may compete much less than expected by established theory.

The paradox of the plankton

RDH offers a novel interpretation of biodiversity theory's great puzzle, the 'paradox of the plankton' (Sommer, 1999). Still hotly debated (Huisman & Weissing, 1999; Lundberg *et al.*, 2000), the plethora of phytoplankton species in the oceans violates classical theory that competitive exclusion limits the number of species to the number of different resources (Gause's law). Intriguingly, plankton and their resources are temporally and spatially variable (Abraham, 1998), suggesting a role for RDH. RDH predicts biodiversity can be higher than expected even in equilibrium conditions, and without invoking other explanations such as chaotic dynamics (Huisman & Weissing, 1999). Consequently, we predict that guild biodiversity covaries with spatio-temporal variability and richness of resources, which is closely related to existing experimental findings (Descamps-Julien & Gonzalez, 2005). The RDH offers a novel explanation for instances of the lack of competitive exclusion elsewhere in nature, where resources are heterogeneous, leading to biodiversity greater than predicted by traditional theory (Sommer, 1999). Furthermore, by showing that competition between species exploiting the same resources can be reduced, RDH provides a mechanism for decoupling the interspecific competition constraints on species richness, as suggested by dispersal-assembly theories of biodiversity (Hubbell, 2001).

Biological invasions: RDH and colonization

Another area that has focused on how and when an environment supports increasing numbers of species is biological colonizations and invasions. While this raises many new issues, a key emerging idea is the so-called 'fluctuating resource availability theory of invasibility' (Davis, Grime & Thompson, 2000). If resources were uniform, space should be divided up such that new invading species ('secondaries', in RDH terms) are unable to extract additional resources from the environment because of competitive exclusion. However, if (and usually because) resource availability varies temporally and spatially, 'pulses' of resources can represent a surplus for extant species and allow sustenance for invasive species on top. Following a variety of supportive empirical tests, Davis *et al.* (2000) concludes that the theory has 'proven to be strikingly robust at multiple spatial scales' (Davis, 2009, p. 41).

RDH and the diversity of large carnivores

While insights for biodiversity theory in general are particularly intriguing, three specific mechanisms suggest RDH can also support the coexistence of species closer to the taxa of its origins: large carnivores.

First, resource patches may enable groups when a food ‘package’ that satiates one predator leaves enough over for others – a zebra kill can feed multiple members of a lion pride. However, these ‘others’ need not be conspecifics. They can be different species. In the Serengeti, jackals and hyaenas scrounge from lions (including crunching up the bone), and the logic extends to the vultures, invertebrates and bacteria that finish the job off. Each different species has a cascading level of food security, occupying ever-thinner strips along the left tail of Fig. 1a. If the first meal is patchy for the lions, so it is for all the others that follow. Yet, all can coexist in the same area while utilizing (at least sometimes) the same food patches. This is RDH. The only difference is that patches support multiple individuals of different species as well as multiple conspecifics. Sometimes, this domino effect is strong enough that secondaries search for predators instead of food itself: jackals seek out lions rather than zebras, arctic foxes seek out polar bears rather than seals, and Eskimo seek out herons rather than fish. RDH can shed light on behaviour and interactions as well as underlying food dispersion.

Second, besides scrounging, Sarah Durant (1998) has suggested that the spatial heterogeneity of resources is critical for species of lower competitive ability to coexist (notably cheetahs and hunting dogs, in this guild) because they can locate and feed on rich but dispersed patches before or without competitors finding them. A cheetah can sometimes eat in peace, but at other times is quickly harried off a kill. The location of other predators therefore becomes as important as the prey. As Durant notes, the distribution of competitors – packs of lions and hyaenas – are themselves clumped, complicating space use but reinforcing the importance of clumped distributions of (multiple) features in the environment for the social organization of any species (Durant, 1998). Cheetahs have to find clumped prey and avoid clumped competition, throwing multiple dice and paying the price of a fairly low food security (and correspondingly low reproductive rates). Note that, by contrast, lions can benefit from having subordinate predators in their territory – sometimes, they do the work of killing prey for them.

Third, overlap with other species can have lower fitness costs than overlap with conspecifics. Same-species secondaries compete for food and mates. Other species only compete for food. The tolerance of ‘secondaries’ of other species should therefore be greater than the tolerance of members of the same species (*ceteris paribus*), making the RDH more powerful in supporting biodiversity than sociality. Interspecific coexistence does not preclude additional benefits either: individuals of multiple species can not only exploit resources in a common territory, but may even jointly defend it, as happens in mixed-species flocks of birds (Macdonald & Henderson, 1977) or even increase patch number or richness for each other, such as honeyguides finding bees’ nests and honey badgers opening them.

Are humans immune to RDH?

If other animals live on a patchwork planet, so do humans. Resource dispersion is thus no less likely to have played a role

in our own ecology and evolution. The human lineage emerged from forest habitats into open savannah and woodland following climate changes in Africa during the Pliocene. As we saw in Rubenstein & Lovette’s (2007) study, such a shift entailed moving to a more variable environment with within- and between-year periods of drought. New plant foods, game, water sources, shelter and materials also meant our human forebears became reliant on a range of often widely dispersed and variable resources.

Of course, human settlement decisions have complex cognitive and cultural components. Nevertheless, even intelligent organisms must distribute themselves in such a way that maintains access to life sustaining resources. Hunter-gatherer societies are highly dependent on access to resources (e.g. water, food, wood; Dyson-Hudson & Smith, 1978) and exhibit spatial patterns that reflect the underlying distributions of those resources (Lee, 1969; Dwyer & Minnegal, 1985). There is no reason why this basic logic does not extend to human societies today. Although the picture becomes complicated by social, economic and political factors, we show below that the emergence of many such factors are consequences of, or innovations to deal with, this very problem of resource dispersion – notably the sharing, trading and storing of resources.

There are two obvious ways in which the RDH applies to people: spatio-temporal variability (heterogeneity) in the availability of qualitatively similar patches (RDH type IV, in Table 2), and spatio-temporal variation in the availability of patches offering different sorts of resources (RDH type V, in Table 2). Below, we illustrate both types of RDH among the Ache, !Kung and Pitcairn Islanders.

But before diving into the anthropological evidence, let us lay out the logic in an everyday example. Imagine that food security for you and your family necessitates buying a meat pie on 80% of your shopping expeditions (recall the binomial dice throwing in Box 1). Because of unpredictability in the supply and restocking behaviour of food shops and the demands of other shoppers, you may need two, even three, pie shops in your home range. But often, exactly along the lines of Carr & Macdonald’s (1986) binomial scenario of resource dispersion, when you arrive at a shop, you will find a superfluity of pies that can be shared with other members of your community. This vignette raises interesting questions about the meaning of community, the definition of the minimum social group considered by RDH, and distinctions between necessity and luxury, to which we will return below. But the basic analogy stands.

Such arguments actually have a long heritage. Early models of foraging behaviour that linked the spatial dispersion of resources to ranging patterns and territory shapes (Horn, 1968) were found to fit the spatial behaviour of pre-industrial human societies as well (Dyson-Hudson & Smith, 1978). Further work developed Horn’s (1968) model to argue that ‘the “optimal” pattern of distribution for foragers will correlate with the degree of resource patchiness; in particular (1) where resource attributes are less patchy, the “optimal” distribution of foragers is to be dispersed; and (2) where resource attributes are more patchy, the “optimal” distribution for foragers is to be aggregated’ (Dwyer & Minnegal, 1985, p. 111).

Accumulating empirical evidence corroborates the basic model. The !Kung of the Kalahari offered a natural experiment of precisely this hypothesis, dispersing in the wet season when waterholes are plentiful, but aggregating in larger camps in the dry season around permanent waterholes (Lee, 1969). But it is the hunting of meat that provides a striking real-world version of the pie dilemma, and one that is likely to have played out in small-scale hunter-gatherer societies for millennia.

Sharing: patchy resources and egalitarianism in the Ache and !Kung

A recurrent theme of ethnographic studies of hunter-gatherers is that they share food, but not just any food: meat. The pattern is that 'resources associated with higher production variance (e.g. big game) tend to be more widely shared' (Smith, 1986, p.409). Among hunter-gatherers, such sharing has been regarded as so important that it is obligatory (Wrangham, 2009, p.163). Reminiscent of Vehrencamp's bats, it is not directed towards kin (and often deliberately directed away from them), and is remarkably egalitarian, creating a system of insurance whereby any given individual has a reduced risk of going hungry (Boehm, 2001).

Intensive studies of the Ache of Paraguay show that around 3/4 of food eaten comes from someone outside the immediate family, and 'the extent of this sharing is positively correlated with the average package size of resources and the unpredictability of securing them' (Hawkes, 1992, p. 292). The Ache are clearly living in an RDH environment, and this situation favours coexistence. Kaplan, Hill & Hurtado (1990) worked out that the average Ache family produced less than 1000 calories per person on 27% of days, but food sharing brought this down to 3%. If there was no food sharing, an Ache family could expect to fail to reach 50% of its required calories for 3 weeks straight once every 17 years (Kaplan *et al.*, 1990). Mapping this scenario back onto the badgers of Wytham, multiple individuals are able to share overlapping home ranges not because they can all go and feed at rich patches when they become available, but because the 'patches' can be killed, brought home and shared out there. But in both cases, group members' overlapping ranges must encompass enough of these patchy resources to maintain a given level of food security. Carr & Macdonald's dice (Carr & Macdonald, 1986) no longer represent patches, but hunters going out in search of them. If we have enough hunters, we survive.

The importance of patchiness is further supported by natural experiments: (1) the Ache also eat plant food, but these are more predictable resources and are only shared within the family; (2) Ache groups that have moved into more settled 'modern' villages (less dependent on foraging) share mostly with kin or by reciprocity; (3) among bushmen in the Kalahari, resource predictability correlates with observed levels of sharing. Compared with the egalitarian !Kung, the otherwise similar Gana San in the north-east mitigate food variation with small-scale cultivation and (watery) wild melons, and not coincidentally have greater hierarchy, economic inequality, hoarding, polygyny and competition for

status (Cashdan, 1983): '... their social rules regarding sharing and economic equality differ, and these differences track the variance in their food and water supplies' (Cosmides & Tooby, 1992, p. 215).

Meat is clearly important, but its importance was magnified by the human ability to control fire (Wrangham, 2009; as well as by the emergence of weapons and cooperation; Table 6). Cooking food had major implications for nutrition (because cooking can increase the nutritional value of a given food item), and for decreasing resource variance (because cooking can sterilize and preserve meat, extending the period over which it can be found and used). This meant that both patch richness and availability of kills were elevated, increasing the food security of both 'primaries' and 'secondaries' – further enabling or enlarging social groups.

Trading: specialization among the Pitcairn and Easter Islanders

Moving beyond subsistence economies, resource dispersion continued to have important effects on the social organization of emerging human civilizations, but new phenomena emerged to deal with it. The Polynesian community of Pitcairn, Henderson and Mangareva islands illustrate the point. Each island offered their inhabitants different essential but sharable resources. Mangareva provided oyster shells, Pitcairn provided volcanic glass and the unique selling point of Henderson may have been live sea turtles. Weisler's (2002) archaeological excavations uncovered extensive evidence of trade among all three islands, whereby each island's deficiencies were filled by the other islands' surpluses. Even a single Polynesian family sought each of these resources and thus needed a territory (effectively enlarged by trade networks) that encompassed all three islands (Diamond, 2005). The richness of the resources on each island, however, could support many families, which, in RDH terms, created a community between the islanders bound by their shared resource requirements. Diamond (2005) describes a similar case among the Easter Islanders, where different essential resources were scattered, with a stone quarry for carving to the east, stone for tool making in the south-west, beaches for fishing in the north-west, and farmland in the south. Elsewhere, there were nesting colonies to harvest birds' eggs and places to grow crops. Any one Easter Island family needed all these resources, but the islanders did not create intricately sliced, single-family, convoluted territories, in the same way that Kruuk & Macdonald's (1985) hypothetical badgers did not slice similarly convoluted pair wise territories from the mosaic of potential earthworm patches (rather, the badgers formed clan territories around a set of defensible patches providing the resource). Humans are just as constrained by dispersed resources, but trade gives them a new way to access the critical number of patches. The Hotu Iti territory on Easter Island monopolized stone for carving statues – plenty for everyone in that territory, but they had to trade that stone with other territory holders who similarly monopolized fish or crops or birds' eggs.

Table 6 Major developments in human evolution that hinged on changes in RDH parameters, or their management (and thus the amelioration of spatio-temporal constraints)

Development	Heterogeneity	Patch richness	Number of patches	Group size	Reference
Move from forest to savannah	Increased (more variable environment)	-	-	Increased	Johnson & Earle (2000)
Sharing	Reduced (meat sharing as insurance against foraging failure)	Increased (high value meat, and in large 'packet sizes')	Increased (multiple hunters more likely to find 'patches')	Increased	Boehm (2001)
Cooperation	-	Increased (can bring down larger/faster prey, e.g. mammoths)	Increased (easier to find, herd, trap or kill)	Increased	Keeley (1996)
Weapons	-	Increased (can kill larger prey)	Increased (easier to kill even dangerous prey from a distance)	Increased	Churchill & Rhodes ((2009)
Cooking	Reduced (cooking preserves food, reducing temporal variation)	Increased (cooking increases nutritional value)	Increased (more types of food now possible to eat)	Increased	Wrangham (2009)
Trading	Reduced (scarce resources acquired from elsewhere)	-	Increased (patches beyond own territory can be accessed)	Increased	Diamond (2005)
Agriculture (storing)	Reduced (surpluses save food for low seasons/hard times)	Increased (greater efficiency in food production)	-	Increased	Barker (2006)
Urbanization	-	Increased (greater supply and demand)	Increased (multiple patches in small area)	Increased	Batty & Longley (1994)
State formation	Reduced (dispersed resources have a single territory/market)	Increased (via economies of scale; central support)	-	Increased	Johnson & Earle (2000)
Globalization	Reduced (scarce resources usually available elsewhere)	Increased (resources tend to come from largest/cheapest sources)	Increased (all resource patches available can be accessed)	Increased	Baylis <i>et al.</i> ((2013)

The pattern is that successive innovations reduced spatio-temporal variability of resources, or increased patch richness and number, allowing larger and more stable groups.

Were these communities of Pacific islanders exceptional for sharing resources this way? In fact, it seems a universal feature across cultures. Human societies vary widely along many dimensions, but Lee and Daly highlight four characteristics that are shared by small-scale hunter-gatherers worldwide. One of the four is land controlled by kinship groups for which, 'Rules of reciprocal access make it possible for each individual to draw on the resources of several territories' (Lee & Daly, 2004, p. 4).

And what then constitutes a group? Polynesian societies had a range of social subunits, families, extended kin groups, communities, etc. This raises the question of which scale reveals the basic social unit in RDH terms, namely that for which the minimum economically defensible territory is configured. While a single Pitcairn family may have needed access to all three islands, just as any Easter Island family needed access to each resource corner of their island, the smallest economically defensible territory is the one that contains all essential patches, and thereby defines the basic social unit as the super-group of all the islands' communities – the whole society. It becomes clear that a minimum defensible territory providing a requisite level of resource security actually defines the minimum fully functional social unit. While any given badger group must coalesce around a set of patches, human groups can coalesce around single or few resources, as long as they can cooperate with a wider community to get all that they need. This suggests important insights for human behavioural ecology. Just as resource availability determines patterns of social organization and mating patterns among animals (e.g. Davies, 1991), so resources influence what forms of social organization and group sizes human societies can reach – as well as the prospects for cooperation and conflict (Dyson-Hudson & Smith, 1978; Ostrom, 1990). This may be one reason why, despite (indeed because of) variations among habitats, what constitutes an 'in-group' varies considerably in size and meaning across cultures and has often been obscure to researchers (Ross, 1983).

Storing: the Neolithic revolution

So far, we have documented major turning points in the way humans have 'fought back' against the tyranny of resource dispersion: sharing, cooking and trading. But the next change was the most significant of all, with major implications for human evolution and civilization: agriculture (Johnson & Earle, 2000; Barker, 2006).

First and foremost, harvested food could be stored for long periods of time, and saved for hard times or low seasons. Second, large surpluses of food could be generated for many by the work of a few. Key effects of these innovations were to (1) increase food security (allowing larger group sizes); (2) reduce uncertainty (allowing group stability); (3) decrease the number of food producers (allowing the division of labour, so some people could devote their time to other activities); (4) increase the concentration of resources in a given location (allowing settlements in towns); (5) increase the defensibility of resources (e.g. within fortifications) and also, on the other side of the coin, create the opportunity for plunder (Keeley,

1996). If resources were dispersed before (whether food or other resources), now they were tightly concentrated into single vast patches. Multiple individuals could live off the same patch, but they could not divide it up into individual territories because of the extensive cooperation needed to achieve it in the first place. This new landscape of resource dispersion, and efforts to reduce its spatio-temporal variation, powerfully contributed to the emergence of both large-scale cooperation (within-groups) and large-scale conflict (between groups; LeBlanc & Register, 2003; Turchin *et al.*, 2013).

RDH today

While the implications of RDH may seem most compelling for pre-industrial societies (before technology and politics complicate the picture), the same logic continues to be recapitulated in many foraging economies today. For example, lobster fishermen on the 'rocky, fractal coast' of Maine, could set traps anywhere they like by law, but in fact follow strict patterns of behaviour (Ridley, 1996, pp. 229–30, our italics): 'The whole coastline is divided into a series of territories, each of which "belongs" to a particular "harbour gang" . . . each fisherman knows from landmarks on the shore exactly where he and other members of the gang must cease trapping. The territories are so precise that they can be mapped after a diligent questioning of the existing lobstermen.' Now, all this becomes interesting because of the underlying distributions of lobster: 'The territories are jointly owned by the whole gang; there is no individual private property. If there were, the system would be unworkable, because *lobsters move around at different seasons and a small territory that an individual could manage would be too small to be a reliable source of lobsters*. Instead, the members of the gang move their traps at different seasons to different parts of the joint territory, which may cover 100 square miles' (Ridley, 1996, pp. 229–30, our italics). This, once again, is precisely the logic of the RDH. Modern life does not inoculate us from our ecology – we still need access to basic resources and tradeable goods. Their dispersion, therefore, continues to govern our behaviour and social organization, if in new and interesting ways.

Even towns and cities are commonly known in the urban planning literature to evolve 'organically' (Batty & Longley, 1994) because human settlements still grow according to their access to certain resources. Contemporary applications of RDH logic are of course complicated because humans, to some extent, arrange resources around themselves as well themselves around resources – technological innovations allow warping of resource distributions, with pipelines, transport and other infrastructures. However, these are not fundamentally different from hunting and storing discussed above, and can still be conceptualized within an RDH framework by measuring dispersion in economic (transfer) costs rather than Euclidean distances. Certainly, there appear to be underlying principles that cut across cultural and historical influences.

George Zipf (1949) noted that the sizes of cities follow a power law, with the second largest city in a country (by population) being around half the size of the first, and the third largest about a third the size, and so on. This reflects a pattern

found with many other social and natural phenomena. However, what is interesting is that numerous other features of urbanization also follow power laws, but with curves of a different steepness. Geoffrey West, famous for his arguments about universal scaling laws in biology, finds that measures of city infrastructure, such as the number of gas stations in cities and the length of paved roads, also follow a power curve, but with a lower exponent to the sizes of cities themselves (West *et al.*, 1997; West, 1999; West, Brown & Enquist, 1999a,b). Although the recurrence of these scaling laws is remarkable, the fact that the proportion of infrastructural resources (patches) decrease with city size is no great surprise to economists because the argument is that cities generate economies of scale (the larger the city, the fewer of these infrastructural entities needed per capita). What is surprising, perhaps, is that precisely this prediction comes naturally out of the RDH – when resources are clumped together, to the extent that they are sharable they can sustain a larger group size per unit area.

Ever expanding circles: human group sizes, resources and globalization

If the smallest economically defensible territory providing all essential resources for even a single family in the Pitcairn Islands is effectively all three islands, then the entire island community (despite subdivisions into many families and alliances) is the basic social unit. This thought leads us on a journey from Kung! Bushmen to nation states and global trade.

Cashdan (1983), in a paper published in the same year as Macdonald's (1983) original generalization of the RDH, developed descriptions of the ecological basis of bushman society that strongly paralleled RDH. In our examination of !Kung society above, we focused on the remarkable egalitarianism of food sharing, which served to equalize intake of high variance meat availability (increasing food security and supporting larger groups). However, we did not explore how that situation impacts on territorial behaviour or defence between groups, and if so, whether that also corresponded with RDH predictions. Recasting ideas on the cost-benefit basis of human territoriality advanced by Dyson-Hudson & Smith (1978), Cashdan concluded that 'although patchiness of resources has received little attention in this literature, there is reason to believe that it may encourage territorial behavior', at least among the !Kung. Comparing four bushman tribes, she showed that the most territorial were those foraging for resources that were sparse and unpredictable (and these territories also had to be larger to meet demands). While dispersed resources can be shared within the group, through an intricate system of sharing described earlier, hunting grounds themselves must be defended from other groups, otherwise food security is jeopardized. The presence or extent of resource dispersion may therefore represent an important risk factor for conflict. But there may also be ways of expanding ecological access beyond inter-group boundaries, and without conflict.

Despite, or perhaps because of, some level of territoriality in these same bushmen societies, Lee (1979) describes the

sociological importance of alliances formed by the exchange of gifts ('non-equivalent gift exchange') between far-flung bushmen groups. As we saw earlier, in dry seasons, scattered groups often coalesce around key waterholes, so they cannot always be territorial, and sometimes they want to swap surplus goods. If these gifts bind together people who need each other (even if only rarely, perhaps across several years), then they may represent an RDH community (a group of groups). Some alliances may be essential (contractionists), others may be luxuries (expansionists), but these alliances themselves may be insurance policies against hard times in the future. Estimates of Wright's inbreeding coefficient (F_{ST}) are low for the !Kung, further supporting a significant degree of overlap among different groups (Bowles, 2006).

This leads to a question of the scale over which minimal spatial groups function. If Dakota produces corn and California produces fruit, and if people in either state need both, we have the conditions set by RDH to give rise to groups with a minimum sustainable territory including both states. RDH expresses the minimum economically defensible territory in terms of the food (or other resource) security they need. Of course, as human society has evolved, perceived and actual needs have changed. Before colonization, Native Americans survived perfectly well in self-sufficient sustainability in Dakota. However, people could not do so today unless they give up a vast range of commodities they have gained access to (and reliance on) since. In that sense, the modern Dakotan, like the ancient Polynesian's requirement for the resources of three islands, needs resources from far and wide (for food, water, fuel, energy, machines, entertainment). As needs proliferate and change, so the smallest territory that can provide them will change, and generally expand, and before you know it, almost every American needs almost all of America, at least sometimes, and a nation is defined. A step further, and the family that needs both cars (from Detroit) and television sets (from China) needs global territory, which in RDH terms can support a colossal community. Some states and alliances are, at least historically, obviously expansionist (reaching beyond their minimum needs), as revealed by the evidence that they can survive despite fragmentation: consider the Austro-Hungarian, British and Russian empires. In their heyday, the needs of a British citizen might have included minerals from African colonies or spices from India, but these were often expansionist needs (luxuries rather than essentials) and Britain survived without colonies (poorer but just as populous).

However, such fissioning is misleading because while the politics have changed, the flow of resources has not. The distinction between expansionist and contractionist alliances are blurred because the needs of, say, 21st century Scots will necessitate trade with other parts of the UK and indeed with former British colonies (as well as other countries), so the alliance that matters in RDH terms, the minimum social unit, may still need a global territory even for the tiniest Hebridean Island. The old territories of the Scottish clans vary widely in size, and are generally larger in the impoverished environments of the Highlands, but in RDH terms, the question is could they be smaller and still viable. Whatever blend of primary productivity, RDH and expansionism might have

determined the answer in the past, nowadays the answer is yes because with increasing specialization, such that everyone needs everyone else, we are cementing a global territory in which conflict is increasingly costly and cooperation is increasingly cheap. However small a nation, a group or a family, their minimum economically sustainable (if not defensible) territory is, to a good approximation, the world. The logic of economic interdependence is of course a deliberate goal behind the neoliberalization of trade, not least because of the widespread view that more and wider trade means less conflict and war, an association that is predicted by the RDH, and supported empirically (e.g. Jackson & Nei (2014, <http://arxiv.org/abs/1405.6400>]

In conclusion: patchy reverberations

While it was always intuitively clear that RDH logic would apply to any kind of contours in resource availability, the hypothesis was strengthened greatly by Blackwell's (2007) mathematical demonstration that RDH does not need patches, but works wherever there is spatial correlation of resources. In so far as genuinely uniform resources are a rarity in nature, the principle of RDH is likely to shimmer through most natural systems, at least at some scale. At its simplest, the core insight remains that patch dispersion determines territory size (and shape), and patch richness independently determines group size – and hence, counter-intuitively, territory size need not scale strongly or at all with group size (although other factors will of course be important in that relationships as well, such as defence costs). But the reverberations from this core are far reaching.

To end with some of the least studied but perhaps most tantalizing implications, we might ask whether RDH also brings new insights at much smaller and larger scales. At the micro end, it suggests a new way of thinking about how organs and cells exploit resources. A cell must have a nucleus, mitochondria and other organelles within its 'territory', otherwise it cannot function as a viable cell. Yet, numerous processes (as opposed to individuals) are able to share these resources when available. Intriguingly, many of the so-called major transitions of life involved the coming together of collections of individual entities to form larger units – molecules, cells, multicellular organisms, social groups – and at each stage, those entities found ways to share spatially or temporally variable resources that none of them could exploit as effectively alone (Maynard Smith & Szathmary, 1995).

At the other end of the spectrum, the formation of human groups or states containing thousands or millions of people must still somehow encompass the resources its population needs – and change when it does not. As resources have become traded as well as foraged, the development of economies and globalization itself can be seen as a kind of extended RDH, with good implications (for a global village with common interests) as well as bad. Nobel Laureate Elinor Ostrom (1990) argued that collective action problems – likely one of the greatest challenges of the new century – tend to arise over resources that are spatially variable and unpredictable. Where resources are more even and divisible, people can

carve them up into private property. But as RDH would predict, spatially variable and unpredictable resources are precisely the kind that groups can (or sometimes must) share. RDH logic may therefore have had a hand in the origins of private property and the evolution of cooperation, with lessons for the types of dispersed and dwindling resources that we must now work out how to keep sharing instead of destroying or competing for – whether fisheries, food or oil.

Batty & Longley's (1994) study of urbanization argued that economic models traditionally focused too heavily on 'the way the various actors and agencies establish a competitive equilibrium through networks of markets and monetary allocation, such theories being largely independent of the space in which such systems exist and largely suppressing the temporal dynamics of such behaviour in rigid assumptions concerning convergence and equilibrium. Anything which threatens to destroy the elegance of the equilibrium such as the imperfections posed by space and time have been ruled out of court.' The 'imperfections' of spatial and temporal variation are exactly what the RDH was designed to address. We frequently suffer inefficiencies of resource allocation and utilization, from catastrophic power shortages in California, conflicts over water resources in the Middle East, severe inequalities of food distribution around the world, and self-defeating depletion of fisheries and farmland – the 'tragedy of the commons' (Ostrom, 1990; Rogers & Lydon, 1994; Finus, 2001). Precisely as the RDH predicts for animals, changes in the mere spatial and temporal distribution of resources – regardless of their overall quantity or richness – can reduce or exacerbate competition for resources and lead to the fission and exclusion of otherwise shareable space.

The Internet poses a new puzzle: if some resources are now instantly available at any point on the planet, are these resources effectively evened out, allowing people to carve up previously dispersed resources into new 'territories' that would formerly have had to be shared? Or does it merely allow a more effective sharing of resources – digital Pitcairn islanders – that reduces the incentive for private territory and expands the social group? Many new avenues for exploration present themselves.

Whatever the implications of RDH for the contemporary and future prospects of human beings, it seems to have played an important role in how we got here. At base, the RDH may have been critical to the formation and maintenance of social groups, and thus an enabling condition for the evolution of cooperation. But the behavioural implications go further. We stressed the point that humans are able to fight back against the tyranny of resource dispersion (as are some animals, such as food caching squirrels; Table 3), leading to the evolution of behavioural and social innovations that reduce the spatial and temporal variation of resources (whether via sharing, cooking, trading, storing or plunder), allowing larger and more stable groups. These innovations may extend to complex beliefs and cultural phenomena. In Bronislaw Malinowski's classic research among the Trobriand Islanders in the Pacific, he noticed that magical thinking and rituals were dominant in activities surrounding open sea fishing expeditions, which were dangerous and subject to great variation in success or failure,

but absent when men fished in lagoons, which were safer and provided lower but more stable returns (Malinowski, 1961) – a pattern found many times since and now termed 'the uncertainty hypothesis'. Such beliefs might be epiphenomenal (just trivial ways of coping with uncertainty), but a growing literature suggests that such beliefs may have adaptive utility in promoting cooperation and preventing cheating in the collective exploitation of resources (Johnson, 2005; Hartberg, Cox & Villamayor-Tomas, in press). The impact of patterns in resource availability – after all the central preoccupation of most organisms and much of human social organization – may resonate far from the territory and group sizes of animals.

But keeping our feet on the zoological ground, 20 or even 10 years ago, it might have been possible to say that the RDH suffered from a lack of empirical testing. Today, this is no longer the case, with Table 4 detailing 43 species and 70 studies in which predictions of the RDH have been tested (with only five coming out against). Beyond the mere number of studies is the remarkable range of taxonomic groups, habitats and regions represented. More intriguing still is the potential role of RDH in some major dynamics of ecology, including the evolution of sociality, biodiversity, body size, synergistic resource exploitation and biological invasions (Table 5). The same logic reflects key differences between our primate cousins, characteristics of hunter-gatherers societies (reflecting our own ancestral environment), and major transitions in the development of human civilization (Table 6). While the RDH emerged from the study of carnivore spatial groups, it appears to reflect a much more fundamental principle of ecology. If so, it is not surprising that its ramifications should be felt far and wide. Nature is not uniform, and even random distributions generate clustering. The world we and all other organisms inhabit is a patchy one, and the RDH provides a unifying logic for understanding how this shapes societies and reverberates beyond them.

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