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Does the resource dispersion hypothesis explain group living?

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The resource dispersion hypothesis (RDH) asserts that, if resources are heterogeneous in space or time, group living might be less costly than was previously thought, regardless of whether individuals gain direct benefits from group membership. The RDH was first proposed more than 20 years ago and has since accumulated considerable support. However, it is sometimes discredited because *a priori* tests of specific predictions are few, relevant variables have proved difficult to define and measure, and because its assumptions and predictions remain unclear. This is unfortunate because the RDH provides a potentially powerful model of grouping behavior in a diversity of conditions. Moreover, it can be generalized to predict other phenomena, including spacing behavior in nonsocial animals and utilization of resources other than food. Here, we review the empirical support, clarify the predictions of the RDH and argue that they can be used to provide better tests.

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Whether animals live in groups can be influenced by numerous direct benefits, such as cooperative hunting, predator avoidance or alloparental care, as well as by direct disadvantages, such as elevated parasite burdens or infanticide risk [1]. Here, we focus instead on an alternative factor, namely, how the availability of RESOURCES (see Glossary) in the environment influences grouping behavior. Species from across the animal kingdom commonly partition available space to defend exclusive TERRITORIES, the size and shape of which represent some economic

optimum [2,3]. These cannot be constructed at random, however, because resources (such as food, water and shelter) do not occur randomly in space. Behavioral ecologists have long recognized a relationship between social behavior and the distribution and predictability of resources [4–7], and increasing empirical evidence points to resource-based explanations of social organization in a variety of species [8–13]. However, there are few well-developed general models that explicitly consider these factors [14–16].

Increases in overall resource abundance leads to increases in habitat quality per unit area, thus resulting in higher animal densities, and typically smaller ranging areas [13,17]. Resource abundance in itself does not necessarily affect group size, however, because rich territories are typically contracted (or split), such that individuals maintain the former per-capita intake rate [18]. But if resources are HETEROGENEOUS in space or time, then this is no longer necessarily true – proportional increases in average resource abundance might not enable the territory to shrink, because larger areas are still needed to encompass the temporal and spatial variability of these resources. Thus, it is the pattern of resource availability, in both space and time, that influences group size [7,10,19]. Therefore, we need specific theories to model how this occurs, and to predict relationships between resource distribution and social organization. Here, we discuss one such theory, the resource dispersion hypothesis (RDH).

The RDH is a hypothetical model that suggests that, 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, satisfying their resource needs without imposing large costs on each other (Box 1; Fig. 1). The basic idea is that, even a single animal 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. According to the RDH, given a certain PATCH RICHNESS and DISPERSION, this same area defended by the original resident (PRIMARY ANIMAL) is predicted to have an excess of

Box 1. The resource dispersion hypothesis

The resource dispersion hypothesis (RDH) asserts that resources might be distributed such that the smallest territory that will support a primary pair (or whatever is the minimum social unit) might also support additional individuals at minimal extra cost to the primary occupants and without any requirement for cooperation between them. This is because where resource patches are heterogeneous (in space and/or time), primary animals will have to defend a relatively larger area to include sufficient potential resource patches to guarantee some critical probability (Cp_α) of encountering enough usable patches over time [a–c]. Assuming some frequency distribution of availability across all resource patches, one can calculate the proportion of time periods in which the total amount of resources available in a territory will exceed what is needed by the primaries (denoted by Cp_β); it is this excess that enables secondary individuals (willing to live with marginally lower resource security) to enter the territory at low cost to the primary animals (Fig. 1a, main text; Box 2) [a–c]. The distribution of resources (in space and/or time) will determine the territory configuration, but the resource heterogeneity and the total richness within the territory will constrain group size (Fig. 1b, main text). Predictions and assumptions of the RDH model are given in Box 3.

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resources some or all of the time, so that there might often be sufficient resources to sustain additional animals (SECONDARY ANIMAL). Although these additional animals might experience a different level of FOOD SECURITY than the original residents, the RDH mechanism suggests that the resource-based cost of sharing a territory with conspecifics is significantly reduced (Box 2). This shifts the cost–benefit balance toward group living, and offers a novel explanation for why some species live within groups even if there are no obvious functional benefits from doing so (e.g. cooperative hunting, alloparental care or predator defence).

Although the RDH gained rigorous support from mathematical modeling (and those results suggested that it might be applicable to a wide variety of species, environments and circumstances [20]), it has until recently mostly been applied to carnivores. This is an unnecessary restriction, because the RDH potentially has a significant role to play in the explanation of social organization across the animal kingdom, including species that are not normally gregarious, and in those that live in large nonterritorial congregations.

The RDH was initially criticized for lacking falsifiable predictions [21], but there are specific predictions that, in combination, enable valid tests of the RDH (Box 3). Several studies (Table 1) have provided empirical support for the RDH, against one possible refutation [22]. However, most of these do not test specific RDH predictions. Rather, they invoke it as the most parsimonious *a posteriori* explanation of the social spacing pattern observed. We believe that the RDH has not been appropriately tested or applied to

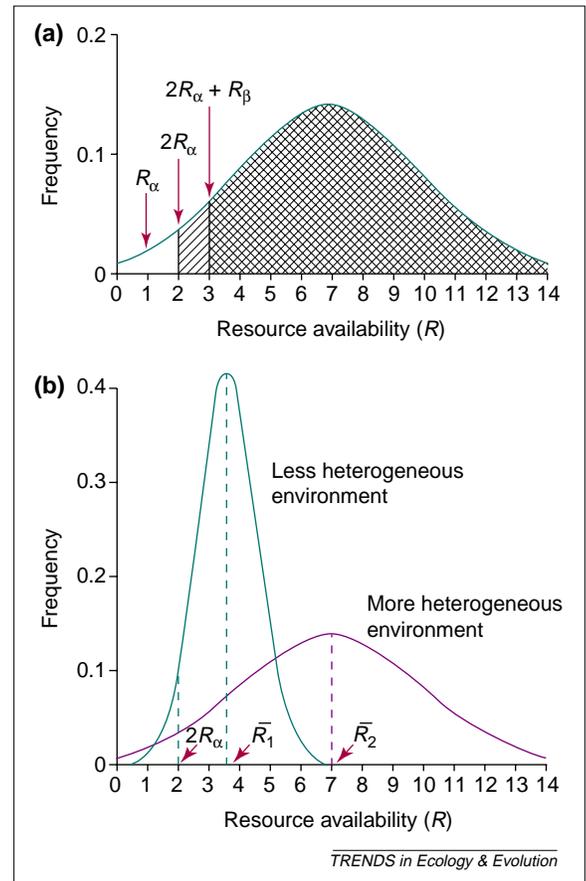


Fig. 1. How the resource dispersion hypothesis works. (a) If resource patches have a certain probability of availability, then several must be simultaneously defended to guarantee some probability of finding enough food for a primary pair of residents ($2R_\alpha$) in a given period. A frequency distribution 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 [46].

the many other species and situations to which it might also be applicable for four main reasons: (1) it is erroneously thought to lack testable predictions; (2) its effects can be masked by more obvious functional benefits of group life; (3) resource distributions are difficult to measure; and (4) its assumptions and predictions are misunderstood (Box 4).

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Box 2. Within-group competition and the resource dispersion hypothesis

Although the resource dispersion hypothesis (RDH) predicts that a territory might contain enough resources for more than just the primary animals, it does not suggest that competition among members of this larger group of animals will be absent. Neither does it require that primary animals dominate secondaries into consuming only 'spare' resources.

The resource-based costs (to primaries) of sharing a territory will be zero only if patch richness is always large enough that a single patch, when available, can support more than the needs of the primary animals (depending on the temporal probability of availability, a minimum territory might require any number of such potential patches). This holds without any assumptions about dominance or other relationships between animals. In other cases where secondary food security is as high as the critical probability for the primaries (Cp_α) (i.e. secondaries experience plenty of food), the costs will be only minor, because, for example, of local consumptive competition leading to increased travel costs. The primaries will still have sufficient food, they might just have to work a little harder to get it.

If secondary food security is lower than Cp_α (i.e. secondaries experience too little food), then potentially there are real costs to the primaries. However, these possible costs relate only to time periods in which primary requirements are satisfied but secondary requirements are not. For example, if primary and secondary Cps are 0.95 and 0.90 respectively, as in Fig. 1a (main text), then only in a maximum of 5% of time periods is there any potential conflict.

It need not be the case, but costs to the primaries can be avoided altogether if they are sufficiently dominant over secondaries that they monopolize resources until they are satisfied (e.g. by eating first). This appears to be common in nature [a]. Feeding competition might be

further reduced by flexible feeding group sizes, which become large only at rich patches [b–d]. Lastly, any costs of conflict over resources should be weighed against the alternative costs of eviction of a potential group member, as well as any general benefits from increased group size.

In summary, the RDH has no specific assumptions or predictions regarding feeding group size or within-patch dominance [e]. The theory applies across the spectrum from group feeders with strong dominance hierarchies, to solitary feeders with no dominance relationships. Within-group competition is not necessarily absent, but by showing how the cost to a primary of sharing its territory might be lower than expected, the RDH nevertheless shifts the cost–benefit analysis of eviction versus tolerance towards group living.

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Why might the resource dispersion hypothesis be commonly applicable?

The resource dispersion hypothesis and spatial variation
The RDH will potentially play a role wherever resources are heterogeneous at a relevant scale. Here, we argue that this will be a relatively common situation. Virtually no resource in nature is homogeneously distributed (i.e. spaced evenly across

space). At a very simple level, therefore, the uneven distribution of resources should be an important factor in how animals use their environment. Nonhomogenous distributions can be further separated into those that are either random, or consistently patchy (or 'clumped'). Patchiness arises from aggregation that is greater than that expected by random processes alone, and statistical tests are

Box 3. Predictions and assumptions of the resource dispersion hypothesis

The resource dispersion hypothesis (RDH) has four specific predictions [a–c]: (1) group size does not correlate with territory size. Instead, (2) territory size is determined by the dispersion of resources, whereas (3) group size is determined by the heterogeneity; and (4) by the total richness of those resources. The following assumptions of the RDH are relatively simple, and are probably met by many vertebrate social systems:

- In heterogeneous environments, primary animals cannot match the resource availability of a territory to their exact needs over time. Thus, there is often (or always) some excess. For simplicity, it is usually assumed that the availability of resources can be described by some probability distribution for the total yield of discrete 'feeding periods' (e.g. a single day or night), which are usually, but not necessarily [b], independent.
- If there are good-quality vacant territories nearby, then secondary animals need not overlap with primaries on an existing territory [d], no matter how low the RDH predicts the energetic costs of this overlap to be. The RDH thus implicitly requires some cost of dispersal to encourage secondaries to join the group [a,c] (or, alternatively, some marginal benefit of group membership, such as helping related offspring).
- Because RDH models were not explicitly spatial [b], territory size was equated with the number of patches within it to reach the prediction that group size and territory size are independent. This assumes that the spatial dispersion of patches is independent of their richness.
- All individuals within the group can potentially utilize any part of the territory, and the whole territory can be traversed during the

relevant timescale (e.g. one feeding period). If not, total resource availability for the territory as a whole is no longer strictly relevant (neither is the representation in Fig. 1a; main text). The RDH still exerts an effect if these two points are not strictly met, although perhaps to a reduced degree.

Bacon *et al.* [b] found that RDH predictions were robust after changing parameter values for distributions of patch richness, assumptions about the time over which the territories are maintained, the number of different resource types exploited, and the relationship between the mean and variance of the yield of a territory. As a result, those authors concluded that the RDH was likely to apply even where there are complex processes of group and territory formation. Nevertheless, because the above assumptions can affect RDH predictions [a–c], they should be subject to verification in any empirical test of the hypothesis.

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Table 1. Empirical studies testing or supporting the resource dispersion hypothesis

Species	Location	Predictions fulfilled ^{a,b}				Refs
		TS ~ GS	PD ⇒ TS	PR ⇒ GS	H ⇒ GS	
Red fox <i>Vulpes vulpes</i>	Switzerland	-	-	-	-	[33]
	Saudi Arabia	-	-	-	-	[34]
	Israel	-	-	-	-	[34]
	UK	Yes	-	-	-	[10]
	UK	-	Mixed	Mixed	-	[22]
Arctic fox <i>Alopex lagopus</i>	North Pacific	Yes	-	-	-	^d
Blandford's fox, <i>Vulpes cana</i>	Israel	-	Yes	-	-	[35]
Crab-eating zorros <i>Cerdocyon thous</i>	Brazil	-	-	-	-	[36]
Silver-backed jackal <i>Canis mesomelas</i>	East Africa	Yes	-	-	-	[10]
Domestic cat <i>Felis sylvestris</i>	UK	Yes	-	-	-	[10]
Badger <i>Meles meles</i>	UK	Yes	-	-	-	[10]
	UK	Yes	Yes	Yes	-	[37]
	UK	-	-	-	No ^c	[38]
	UK	Yes	Mixed	Mixed	-	[23,39]
	UK	-	Yes	-	Yes	[40]
Spotted hyaena <i>Crocuta crocuta</i>	Norway	-	Yes	-	-	[41]
	Tanzania	-	Yes	-	-	[18]
Kinkajou <i>Potos flavus</i>	Panama	-	Yes	Yes	-	[42]
White-nosed coati <i>Nasua narica</i>	Costa Rica	-	Yes	-	Yes	^e
Capybara, <i>Hydrochoerus hydrochaeris</i>	Venezuela	-	-	Yes	-	[43]
Mara <i>Dolichotis patagonum</i>	Argentina	-	-	Yes	Yes	[44]
White-throated magpie jay <i>Calocitta formosa</i>	Costa Rica	-	Yes	Yes	-	[30]
Alpine accentor <i>Prunella collaris</i>	Pyrenees	Yes	-	-	-	[45]

^aAbbreviations: -, not tested; GS, group size; H, heterogeneity of resource availability in the environment; PD, patch dispersion, PR, (mean) patch richness; TS, territory size or group home-range size (See Box 3 for detailed explanation of predictions).

^bRelationships between variables: =+, positive correlation; ~, no correlation.

^cThis study tested for a correlation between heterogeneity and territory size rather than group size. This is a poor prediction of the resource distribution hypothesis because if heterogeneity is increased (and other variables are kept constant), primary food security need not change (Fig. 1b), so one would not predict a change in territory size (if anything, one would predict a negative relationship because in the more heterogeneous case average resource availability is higher).

^dGoltsman, M. *et al.* (unpublished).

^eValenzuela, D. and Macdonald, D.W. (unpublished).

needed to distinguish the two [23] (Box 4). The RDH model is based explicitly on patchy distributions, and suggests that the costs of sharing an area will be low when the resources are sufficiently patchy and rich.

Patchiness itself, rather than randomness, is likely to be common in nature because of its dependency on the scale at which an animal uses resources in its environment [24,25]. Even if some resource – such as fruiting trees – are apparently randomly distributed in their own habitat, at a larger scale, a frugivore might experience them in patches. For example, suppose that a species of fruiting tree was randomly distributed within wetland habitats. A bird that specialized on these fruits might perceive this food resource as patchy, because it needs to feed at several such trees each day, and the wetlands in which it forages are broken up into patches over the broader landscape by intervening areas of grassland, rocks and upland forests.

Thus, patchiness might commonly result at a spatial scale relevant to the daily home range of animals, even if the resource itself is not apparently patchy at finer scales. This effect can be illustrated for a variety of organisms, by using a generalized hierarchy of scale that classifies food resource patches

as either 'bites', which influence individual foraging decisions [26], or 'meals', which influence daily home ranges [25] (Fig. 2). These two levels are pertinent to the RDH, given that bites reflect individual patch richness (e.g. individual ripe fruits on a tree), and meals reflect the daily food resources required from the territory (e.g. the total number of fruit trees visited on a typical day). A consideration of both of these levels suggests that patchiness might be more common than is initially apparent for various types of animals. Even if at local scales prey are random (constituting 'bites' during foraging), once these prey distributions are considered on a larger scale relevant to satisfying the daily energy requirements of the individual eating them (constituting the 'meals' obtained from the sum of that day's foraging activity), they are patchy. Significantly, meals correspond to the scale of the territory; hence the patchiness that emerges is at a scale that is directly relevant to the RDH (and to the economics of resource defensibility).

The resource dispersion hypothesis and temporal variation

Resources in the environment can also be patchy in time. Thus, animals might have to defend larger

Box 4. Potential misinterpretations of the resource dispersion hypothesis

Patch independence

Most detailed models of the resource dispersion hypothesis (RDH) assume patches to be independent (in availability or yield). This simplifies the calculation of the distribution of total yield over all patches. Independence is not necessary, however. Positive dependence among patches might even lead to a stronger RDH effect, because it increases the effective patchiness of the environment [a].

The probability distribution of resources

The shape of the probability distribution of resources (as in Fig. 1a; main text) is not crucial. Such an (approximately) normal curve will be common in reality [especially when total yield is the sum of yields from several patches by virtue of the central limit theorem – whereby means of samples from any distribution (Poisson, exponential, etc.), will themselves be normally distributed]. Nevertheless, other shapes of the resource distribution curve are possible [b], and the idea of the RDH is unaffected. The spread of the distribution is much more important than its precise shape.

Multiple resource types

Davies *et al.* [c] suggested that the RDH should be modified to separate its influence on food from other factors affecting the dispersion of mates. Treatments of the RDH usually imply that the relevant resource is food. However, the logic can be extended to any patchy resource that is also required with some level of security (e.g. shelter, water, mates, or a mixture of different resources). By testing RDH predictions for each potentially limiting resource, one can examine the relative influence of each on social organization.

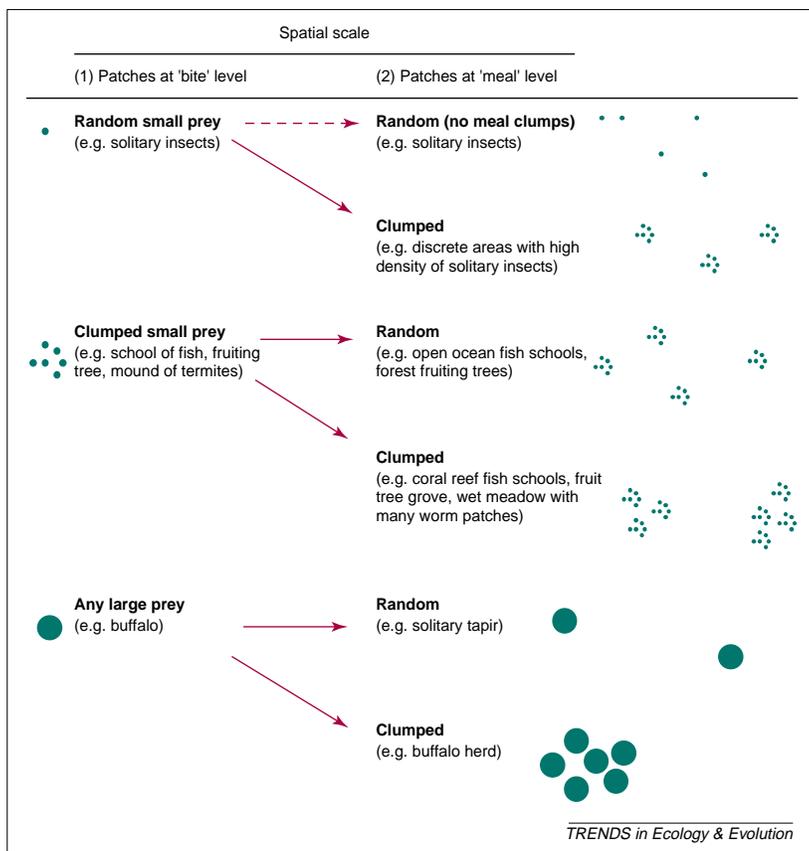
Patch definitions

Resource patches are, compared with the matrix surrounding them, relatively small areas with relatively rich resources. Ecologists now realize that the world is patchy, and that the perception of these patches is inherently dependent on scale [d]. Patches of resources are sometimes obvious, other times they require statistical tests to identify. For example, a fruiting rainforest tree or a school of fish in the open ocean would both be obvious patches. But a loose congregation of earthworms, or an area

of forest particularly rich in squaw root (a favorite food of the American black bear) are less obvious, and might only be uncovered and defined by statistical analysis of distributional data [e,f]. Although RDH predictions and assumptions apply to both obvious and hidden patches, RDH effects will be stronger the further one moves along the continuum towards distinct patches. Similarly, it might have a more pronounced effect if the matrix in which the patches occur is entirely empty of resources, rather than containing resources of low density or quality [g]. Resource distribution and abundance are notoriously difficult to measure over relevant time scales [e,g,h], and might take as much field effort as the studies of the animals that use them.

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areas to include resources needed at different times. Depending on the temporal nature of the resource, this could be food patches that become available at different times of the day, nightly protective dens and daily water sources, tree species that fruit at different times of the year, and/or mineral licks that are needed only at certain times of the year. According to the RDH, some of these resource patches might be rich enough to support more than just the primary pair, but because of their spatiotemporal heterogeneity, primaries must defend larger areas that encompass this variation. This might be important simultaneously at a variety of scales (e.g. hours, days, weeks, months or years), as suggested above.

Fig. 2. Resource distributions for some typical food types at two (relative) spatial scales. Small quantities of food ('bites') can be random, clumped in space, or clumped within a single large prey organism. For example, groups of small prey often occur in clumps, as does a large herbivore, because it is devoured in many bites. However, even if prey distributions are not patchy at the 'bite' level, they may become patchy at the next scale up (the 'meals' eaten over the whole foraging period) because prey densities vary across space due to numerous non-uniform factors (e.g. microclimate, soils, unusable habitat, such as rocks, within-habitat patchiness, or social aggregation of individuals). For example, groups of small prey could again be either randomly distributed (thus already constituting a patchy resource), or they could occur as collections of patches. An example of a distribution that might not meet the requirements of the resource dispersion hypothesis (i.e. do not arise in patches at either spatial scale), might be small prey that are perfectly randomly dispersed at both scales (dashed arrow).

Table 2. Predicted changes in group size and territory size according to the resource dispersion hypothesis, by experimentally manipulating relevant variables^a

Variable to be increased	Group size	Territory size
Number of animals per territory	+	= (but + if extreme change)
Total resource abundance	+	- (although not necessarily if still dispersed)
Resource distribution (clumped, random, uniform)	(+, =, -) ^b	(+, =, -) ^b
Spatial dispersion (distance between patches)	=	+
Temporal distribution (clumped, random, uniform)	(+, =, -) ^b	(+, =, -) ^b
Temporal dispersion (time between patches)	=	+
Average patch richness	+	=
Variability in patch availability (heterogeneity)	+ (providing overall abundance is the same)	=

^aChanges are denoted by: +, increase; -, decrease; =, no change.
^bDepends on the extent to which resources were clumped in the initial condition.

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Testing the resource dispersion hypothesis

In many social species, the RDH might operate in concert with other factors promoting group living (e.g. group hunting or predator defence). Such obvious functional benefits of group life might mask any underlying effects of the RDH, and those underlying effects might remain difficult to uncover statistically. This does not mean the RDH is not worth testing for, but that the study system should be chosen carefully. For example, it would ideally be known well enough to be modeled precisely, lack other obvious functional benefits of group life and/or be suitable for resource manipulation experiments.

Although the studies in Table 1 provide valuable support for the RDH, manipulation experiments would be the most powerful method of testing for RDH mechanics. Until now, most interest in the RDH

seems to have come from biologists working on wild carnivores, for which such manipulations were difficult to do. An ideal field test must also account for the nonresource factors affecting grouping behavior, which would be simpler in species that live socially in some, but not all, situations. Manipulation of resources could then be tested for effects on group size or territory size as predicted by the RDH (Table 2). It should be noted that not all RDH predictions are unique. Table 3 shows a cross-tabulation of RDH predictions along with the principal predictions of alternative hypotheses for grouping. Although some predictions arise from multiple hypotheses, simultaneous tests of all predictions should, together, distinguish the RDH from the alternatives.

The many potentially confounding variables (and combinations of possible nonindependence among them) might make it difficult to conduct tests of the RDH, but do not make the RDH logically untestable. The RDH does not predict groups to form wherever resources are heterogeneous, or that, in such places, all species are prone to form groups. Other costs of territory sharing (such as increased infanticide risk, parasitism or disease) might have an overwhelming negative influence and, if dispersal is not too risky, then those other costs need not be large. Likewise, in many cases, animals might have evolved behaviors that so increase the merits of grouping (such as alloparental care or communal defence against predators) that they now strive for it irrespective of the RDH (this was the scenario envisaged in Kruuk and Macdonald's term 'expansionists' [18]). This does not alter RDH predictions, but it highlights the potential difficulties of exposing them in experiments.

Conclusions and a future for the resource dispersion hypothesis

The RDH sometimes seems to be viewed as a 'just-so story' for how a particular species ends up in groups if they live in a patchy environment (especially if no direct benefits of group living are discovered). On this basis, the RDH would be classed as a 'tautology' rather than a theory – something that is logically true within a certain set of conditions, but which lacks the power of prediction [27]. However, this interpretation is false. The RDH predicts that the resource-based costs of group size vary with a specific explanatory variable: heterogeneity.

The strongest test of this hypothesis would be in a controlled manipulation experiment in which resource distributions and richness are adjusted to test for predicted changes in group or territory sizes. One recent study (which was not a test of the RDH) found that normally exclusive female dunnock *Prunella modularis* territories could be made to overlap if food was artificially altered to become patchy [28]. Between-population studies also offer potentially strong tests of the RDH in species that vary in their degree of gregarious behavior. Comparative tests will, however, have to confront

Glossary

Critical probability: minimum probability that the requirement of resources for an animal to sustain itself will be available over a given time period. This might be different for primary animals (C_{p_1}) and secondary animals (C_{p_2}).

Dispersion: distance between resource patches.

Food security: the actual probability that the requirement of resources of an animal will be available over a given time period. This might be different for primary and secondary animals.

Heterogeneity: the pattern in which resources are available across space in the environment, defining a continuum from homogenous resources (where resources are evenly distributed) to very heterogeneous (where resources are very patchy).

Patch: a spatial aggregation of some resource (Box 4).

Patch richness: (patch size) × (patch density). Although it might be convenient to model them as such, patch size and patch richness are not the same thing.

Primary animals or 'primaries': original resident animals forming the 'minimum social unit' of a territory (e.g. a single individual, a breeding pair, or a larger cooperative group). Regardless of the initial unit, it is group size variation above this minimum that is hypothesized to be affected by the RDH.

Resource: something from the environment that an animal needs, typically food, water, or shelter sites.

Secondary animals or 'secondaries': additional animals sharing the territory of the primaries.

Territory: a defended home range, either by a group, a pair or a solitary individual.

Table 3. Predictions of the resource dispersion hypothesis compared with other resource-based models for social organization

Model	Model predictions ^a								Refs
	GS=+Mates GS varies depending on mate dispersion	TS=+Mates TS correlates with mate dispersion	TS=-GS TS independent of GS	TS=+PD TS correlated with patch dispersion	TS=+RA TS correlated with resource abundance (or renewal rate)	GS=+H GS correlated with heterogeneity (patch variability)	GS=+PR GS correlated with total richness of patches	GS=+RA GS correlated with resource abundance (or renewal rate)	
Early models									
Mating systems in general	x	x							[14]
Weaver birds social organization	x	x							[7]
Primates and food resources			y			x			[4]
Bats			y	x			x		[6]
Recent models									
RDH	y	y	x RDH (1)	x RDH (2)	y	x RDH (3)	x RDH (4)	y	[46]
Null model (noise) ^b			x						-
Resource abundance hypothesis ^c			y		x			x	[12]
Territory inheritance hypothesis ^d			y				y	y	[47]
Constant territory size hypothesis ^e			y				y	x	[48]
Prey renewal hypothesis ^f			y	y	y		y	x	[11]
Terrestrial herbaceous vegetation hypothesis ^g			y		y		x	x	[8]
Patch size hypothesis ^h			y				x		[8]
Temporal food availability hypothesis ⁱ			y			x			[49]

^a x denotes where a given model makes a specific prediction. y denotes where a prediction might also plausibly be found in field tests, even if not a principal prediction of the associated hypothesis (this would depend on circumstances and details of the environment). Numbers within the resource distribution hypothesis (RDH) predictions correspond to those used in Box 3. Blank boxes indicate that the given model makes no specific prediction. For relationships between these variables: =+, positive correlation; =-, no correlation. Abbreviations: GS, group size; H, heterogeneity; PD, patch dispersion; PR, patch richness; RA, resource abundance; TS, territory size (See Box 3 for details of the RDH predictions).

^bAlso predicts a lack of relationship between territory size and group size, which could be found to be unrelated due to any number of confounding variables (e.g. statistical noise).

^cSuggests that group sizes are larger where resources are more abundant (per unit area), because with higher resources per unit area, exploitation competition costs from group members also foraging in the same location are reduced. [12]

^dSuggests juveniles might remain in the natal territory and result in a group when dispersal is costly relative to feeding competition costs at home [47]. Assumes that there is no cost to having a territory large enough to sustain additional animals when this occurs, and therefore requires some other auxiliary mechanism, such as the RDH, for the origin of group living [50]. Its predictions concern the relative costs and benefits of dispersal versus feeding competition at home, but there are certain RDH predictions that might also be expected under this model.

^eProposes that, if food availability fluctuates in time, animals that defend fixed territories will be able to tolerate additional group members at low cost when food happens to be abundant [48].

^fSuggests that, if prey renews very rapidly then, in a given area, food is replenished fast enough to preclude interference or scramble competition, several individuals may be able to coexist without competition [11].

^gSuggests that where terrestrial herbaceous vegetation is available in between the main feeding patches of primates (usually fruit trees), feeding competition might be reduced, thereby enabling larger group sizes to form [8]. The idea of utilizing the interpatch habitat matrix is an important one that is more realistic than the assumption of interpatch redundancy (floating food patches in an otherwise useless space) [35,46].

^hSuggests feeding competition might be lower where food occurs in larger patches [8] (here, by larger, it is meant a greater amount of food per patch). Thus, group sizes might simply be determined by the size of the average (or minimum) patch.

ⁱSuggests that group sizes are adjusted to the minimum resource levels during the year: populations that experience seasonal food shortages should have smaller group sizes than those with approximately uniform food availability [49].

the problem of deriving accurate and comparable indices of resource heterogeneity and richness.

Such experiments remain to be done because, until now, interest in the RDH has focused on large, often protected mammals, such as the European badger *Meles meles* or red fox *Vulpes vulpes*, which makes manipulation difficult. The best that these mammal studies can do is to find (or not find) predicted correlations between the relevant variables. However, these correlative studies are meagre tests of the RDH because (aside from measurement problems, small sample sizes and Type I or Type II error), an absence of evidence for

the RDH is not evidence of its absence. Nonetheless, the increasing support from field studies suggests that the hypothesis deserves more attention, even if it has defied a neat test. Testing the RDH might be difficult, but it is certainly not impossible. There are clear predictions to test and the problems of measurement can be overcome by careful selection of variables and methodology [29].

Studies into the mechanisms predicted by the RDH are important not only because of their relevance to grouping behavior in territorial species, but because the same principles might have wider application. First, although devised to explain why

group living occurs, the RDH also offers a formal explanation of how resource distributions might affect the size and shape of non-social animal territories [30]. Second, although our discussion focused on species that defend territories, the RDH also applies to animals that do not, showing how nonterritorial individuals might overlap in space use with fewer resource-based costs than otherwise expected (given certain resource distributions). Finally, the importance of testing RDH predictions in the field is highlighted by the fact that heterogeneous

resources are being increasingly integrated into theory about complex social behavior in a variety of species (e.g. human spacing patterns [31], culture in cetaceans [32]), whilst empirical studies are left lagging behind.

Models that give poor explanations of reality should be rejected in favor of alternative models. It is our belief, however, that the RDH has yet to be subjected to rigorous testing and therefore lacks any good reason to reject it. Now, at least, we hope to have pointed out what needs to be done.

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