

## *Sentenced without trial: reviling and revamping the Resource Dispersion Hypothesis*

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The resource dispersion hypothesis (RDH) offers a predictive model for how, in heterogeneous environments, some animals may form groups even without any direct benefits from doing so. Revilla (2003) levels a number of criticisms at the RDH, all of which we feel can be easily clarified or resolved (we address them in the order they appear in his critique). We argue that the RDH, despite its long history and despite our own efforts, still lacks convincing evidence to reject it. On the contrary, we see it as having weathered its critics very well. While there is steadily accumulating evidence in support of the RDH, there are very few empirical tests that provide decent evidence against it.

During his Master's degree, one of us (DDPJ) wrote a highly sceptical essay hacking away at assumptions of the RDH and arguing that it did not, on its own, provide a satisfactory explanation of sociality. Five years later, after thinking about it and working on it most of the days in between, he still holds those same views. However, one thing has most certainly changed. He is now convinced that good tests of the RDH (either trying to demonstrate or to falsify it) have simply not been done. As a result, theoretical arguments against the RDH remain essentially ineffectual because, even if it can be postulated that certain aspects of the RDH model seem unlikely (or unimportant), it remains to be demonstrated that these shortcomings are the case empirically. That is the challenge we still face.

The underlying logic of the RDH still holds as relevant now as it did when it was first conceived (Macdonald 1983a), or when it first appeared as a formal model (Carr and Macdonald 1986), or when it was corroborated by more rigorous mathematical modelling (Bacon et al. 1991). After a critique published soon after the original paper (von Schantz 1984), the RDH – in its more developed theoretical form – remains unattacked

by any published theoretical criticisms. Empirically, there has only been one study we know of (until Revilla's work) that claims a falsification of RDH predictions (Baker et al. 2000), and their conclusions have been questioned (Blackwell 2001). But it is important to realise that, even if there were studies successfully falsifying the RDH in this or that location, or in this or that species, they would not provide good reason to reject it as a model elsewhere. As Roger Peters was at pains to remind us (Peters 1991, p. 53):

'In theoretical ecology, the logic of the models is not disproven when they fail to describe an ecological phenomenon, for failure only indicates that the premises of the model did not fit the ecological system to which they were applied. Mismatches of model and observation are not counted as disproofs, but as indicators of limitations which may eventually describe the domain of a yet unarticulated theory. Models become theories when we have enough experience to predict when they will apply and when they will not. Until we gain this experience, the models are safe from disproof.'

### **A model debate**

#### **What isn't the RDH?**

Revilla's (2003) characterisation of the RDH in his first paragraph is incorrect. He suggests that the primary assumption of the RDH is that the single resource on which the hypothesis is exclusively based is food. This was commonly the resource deemed most obvious and useful for illustration, but it was made clear in original versions of the model, as well as more recently, that the dispersed resources in the model could be anything (Carr and Macdonald 1986, Johnson et al. 2002b). In any case, the RDH does not rule out other, non-resource based factors that might be acting simultaneously; it is not a mutually exclusive hypothesis.

Revilla then cites a second assumption of the RDH: 'key habitats holding key food resources have a heterogeneous spatial distribution' (he restates this later 'RDH has several assumptions, such as a patchy spatial distribution of food resources'). This statement is vastly misleading. In no way does (or could) the RDH assume resources are heterogeneous. Rather, the RDH is a model limited to those cases where resources are known, *ex ante*, to be heterogeneous. Thus, heterogeneity is a pre-requisite of the RDH as an applicable model, not an assumption of it. Indeed, if resources are homogenous, it was always implicit in the hypothesis that 'the area that provides minimum requirements for a pair will not support additional adults' (Macdonald 1978, p. 417).

A third assumption Revilla identifies is that individuals 'must maintain the smallest economically defensible territory which encompasses sufficient food resources.' This is certainly often cited in the RDH literature. But the RDH does not assume that any animal 'must' do so, rather it suggests what can happen *if* they do. However, it is also misleading for another reason; RDH effects would not simply disappear just because focal animals did not minimise their territories (behaving as 'contractors' in the terminology of Kruuk and Macdonald 1985). Rather, the RDH postulates 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' (Johnson et al. 2002b, p. 564, Box 1). This is only a paraphrase of the earliest formulations and is not a shifting of ground, e.g. Macdonald (1983a, p. 379) wrote that 'where resources are heterogeneous the resource dispersion hypothesis suggests that the smallest home range with an economically defensible configuration which will reliably support a pair of red foxes (on a bad night or a bad year) may sometimes support additional foxes'. In other words, the RDH is often framed in this way to focus on the notion that additional animals may be supported *even in the extreme case* of a primary animal's *minimum possible* territory. Yet, where a territory is larger than such a minimum, group sizes could be even higher still, at least partly on account of the same RDH mechanism in which patchy resources result in territory-wide surpluses. Indeed, surpluses would be more common in larger territories, especially 'expansionist' ones (in Kruuk and Macdonald's, 1985, terminology), since in those cases animals expand for reasons other than food and are therefore not primarily interested for themselves in the incidental extra food. Ethiopian wolves appear to be an example in that while they tend to expand their territories, their smallest ranges nonetheless can sustain a group.

### What are the relevant alternatives?

Revilla's (2003) table of hypotheses for the origin of sociality is misleading (see his Table 1). The 'main constraints and assumptions' for the resource dispersion hypothesis are incorrect. As explained above, the statement that under RDH, 'territoriality is only affected by food resources' is invalid. Second, that 'key habitats holding key resources have a heterogeneous spatial distribution' is neither a constraint nor an assumption, only the situation in which RDH is postulated to function (and, in fact, the habitats themselves need not be heterogeneous, since resources could be heterogeneous within them; Johnson et al. 2001b). Third, Revilla's further claim that the RDH assumes that resources are 'patches scattered in otherwise barren areas,' is completely mistaken, since the matrix between 'patches' certainly need not be empty of resources. This was made clear in early discussions of the RDH (Macdonald 1981, Carr and Macdonald 1986, Macdonald and Carr 1989) and more recently (Johnson et al. 2002b). As for other hypotheses that Revilla cites, the 'den site hypothesis' (Doncaster and Woodroffe 1993) has been questioned using a more sophisticated analysis of the same data (Blackwell and Macdonald 2000; but see Doncaster's 2001 reply), and the 'passive range exclusion hypothesis' (Stewart et al. 1997) is not a hypothesis for the 'origin of sociality,' it is a hypothesis for the maintenance of certain aspects of territoriality.

### Why hasn't the RDH been refined?

Revilla finds it 'surprising' that there has been little 'refinement' of the RDH in its long history. This appears to suggest to him that it does not conform to the usual pattern of theory development. However, as he notes, empirical data are needed (indeed are a pre-requisite) to allow refinements. The whole point of our research agenda has been to address the remarkable *lack* of empirical data, hence the limited refinement. We agree refinements are crucial, but disagree that good enough information exists to demand them (or to identify consistently what they might be). The RDH's original assumptions and predictions remain to be tested convincingly.

In fact though, *theoretical* refinements have been made. The RDH model was refined in a more rigorous mathematical model (with continuously, rather than discretely varying resource patch richness), which found that original RDH predictions were upheld, and that various changes of key assumptions did not alter those predictions (Bacon et al. 1991). Finally, it is possible that concerns over RDH assumptions are over-rated, given a recent study which suggests that the RDH may work even without definable patches, simply due to the emergent properties of spatial correlations in resource abundance across space (Blackwell 2001).

## What does the proliferation of alternative hypotheses mean?

Revilla is absolutely right to point out that other, alternative hypotheses exist and should also be tested. But we disagree that the 'large number of alternative hypotheses shows that the RDH has been considered as a weak (or unproven) explanation of group living by many authors.' For a start, the RDH can never be 'proven.' Moreover, we would dispute the notion (implied by Revilla) that there should be a correlation between the number of theories for a phenomenon and the lack of an accepted explanation for it. For example, a multitude of theories persist for the origins of life on earth, even though science appears to have come up with a compelling but 'unproven' one. An alternative reason for why the RDH has prompted a multitude of alternative hypotheses is precisely because people have failed to test it satisfactorily or appropriately. For example, researchers often 'test' the RDH in vastly different ecological conditions from that in which it was formulated, not because it was deemed a potentially good model (the correct criteria) but because those researchers were studying the same species as those in former RDH papers (the wrong criteria). The RDH is specific to heterogeneous environments, not species. Consequently, when the RDH appears not to work, researchers have tended to invent new explanations (which might be good ones), but falsely see them as alternatives to the RDH.

## Individual variation

Revilla correctly notes that different individuals may have different strategies from each other (e.g. males, females, old, young, dominant, subordinate). Unfortunately, few data exist on whether all individuals are able to use the whole groups' range, or whether they do so in the same way, but it certainly remains a key question to determine. We know that dominant and subordinate crab-eating zorros, *Cerdocyon thous*, use group ranges differently (Macdonald and Courtenay 1996), as apparently do some radio-tracked badgers (Revilla and Palomares 2002). Kruuk and Parish (1987) noted that individuals increased their percentage use of the entirety of the group territory as food decreased. It is important to note however, that even if individuals do use different parts of the territory, or use it in a different way, that does not detract from the fact that heterogeneous resources may lower the costs of group living (below whatever the 'baseline' might be for a given situation). The constraints of territory formation on the primary animals remain. In any case, among badgers, although there are possibly dominance hierarchies in breeding, there is no evidence for dominance hierarchies in competition for food (Macdonald et al. 2002).

## Costs and benefits of dispersal are integral to the RDH

Revilla is correct to note that (normally, at least) 'groups form due to the philopatry of young animals'. However, he suggests that a 'problematic assumption of the RDH is that these philopatric individuals incur no additional cost when remaining in their natal territories'. It is crucial to realise that the RDH does *not* suggest costs of secondaries (additional individuals joining the territory) are zero. Under some model conditions they could be, but it need not be the case and the RDH will operate under the more likely condition that such costs do exist, but just at a reduced level. This is explicit in other papers (Carr and Macdonald 1986, Bacon et al. 1991, Johnson et al. 2002b). In the work of Macdonald and Carr (Carr and Macdonald 1986, Macdonald and Carr 1989), for example, the marginal advantage of staying to become a group member is explicitly considered – the point is that offspring will stay when the cost/benefit ratio makes it advantageous to do so, but that RDH effects will influence this balance.

Second, Revilla notes that philopatry entails the costs of missed reproductive opportunities, which must therefore be weighed up against any advantages of staying at home (such as reduced feeding competition due to the RDH or some other mechanism). As a result, 'any theory aiming to explain group living must deal with the causal mechanisms affecting the decision of individuals when dispersing or remaining at home'. We are glad Revilla raises this, as we suspect this may have been under appreciated in previous RDH papers, although it was quite plain in, for example, Macdonald and Carr (1989) and is specifically revisited by Walters and Blackwell (2002). We have recently discussed dispersal as an implicit assumption of the RDH (Johnson et al. 2002b, Box 3), and suggested this to be a critical factor in determining why badgers are social in some, but not all parts of Europe (Johnson et al. 2002a, p. 422–423):

'Even in an 'ideal' RDH habitat that potentially allowed many individuals to share the territory of a primary pair, juveniles should still disperse if possible [that is, if it pays off] (1) to establish their own territory and thus achieve a maximum guarantee of food security and, (2) to avoid incest and search for mates (Baker 1978, Harvey and Ralls 1986, Johnson and Gaines 1990). Thus, dispersal is only prevented where densities are high enough to incur such costs to dispersal that they outweigh the benefits (Macdonald and Johnson 2001). Whatever the particular mechanism allowing groups to coexist, be it the TIH [Territory Inheritance Hypothesis], CTSH [Constant Territory Size Hypothesis] or the RDH, no group will form without a disinclination to disperse. Since we know that badgers tend to live in kin groups (Evans et al. 1989, Cresswell et al. 1992), we also know that it is mainly the retention of otherwise dispersing offspring that form the group. There are strong theoretical grounds to expect an ESS dispersal rate of 0.5 even if dispersal mortality is 100% (Hamilton and May 1977, Johnson and Gaines 1990). If this is correct,

then it implies dispersal costs (and thus, by inference, population densities) may have to be relatively high before offspring are retained to form groups, whether that occurs through the RDH or another mechanism.

Therefore, although there appear to be possible examples of the RDH at low densities as well (Macdonald et al. 1999), the high-densities of badgers in the British Isles may be a specific precursor to the operation of the RDH as a mechanism permitting, but not causing, aggregation of individuals within spatial groups.'

This is largely phrased for the case of badgers, but we should point out here that the RDH is not at all limited to kin groups. Indeed, the original studies that sparked the hypothesis were of non-kin groups (bat colonies, Bradbury and Vehrencamp 1976, and red-winged blackbirds, Orians 1961). Revilla comes back to this point later on, suggesting that the 'key question' is 'why individual badgers remain philopatric, and do so in spite of the important costs associated with a reduced probability of reproduction within the group'; again, reproductive suppression is not necessarily part of the story, though it may be in badgers). Given our concordance on the importance of the costs and benefits of dispersal, our argument that Revilla thought 'cannot be accepted on the grounds of the information available on badgers and other animals', can now easily be accepted: 'a patchy spatio-temporal dispersion and richness of food resources might lead to the passive formation and maintenance of animal groups, even in the absence of any direct benefits of group living per se'. From the origins of work on the RDH, it was clear that 'other foxes [or secondaries of any species] are tolerated in numbers and at times when any costs (to the basic pair) due to their presence are outweighed by the overall benefits' (Macdonald 1983a, p. 379).

A final point of relevance here is that if one thinks dispersal is the key variable, and sets out to test it, there is a potential methodological problem in that *behavioural* incentives to disperse may be at variance with the researchers perceived *advantage* of dispersal. Simply put, animals may be hard-wired to kick their offspring out of their territory, or for the offspring themselves to 'want' (or not want) to leave, irrespective of whether they actually need to as a result of resource competition (Balharry 1993). Balharry suggested this as an explanation for why some species do not form groups in new environments despite apparently perfect conditions for doing so. This would represent the maladapted legacy of another environment which they formerly inhabited and, as we speculated before, 'in the medium-term it may override any cost-benefit trade-off in tolerance of conspecifics invoked in models of sociality' (Johnson et al. 2000, p. 187). This may also be part of the explanation for why wild cats do not cluster around food clumps, whereas domestic cats do (Macdonald et al. 2000).

## The prediction of a lack of relationship between group size and territory size

Revilla questions whether the relationship between group size (GS) and territory size (TS) is a 'prediction' of the RDH or not (he thinks it constitutes an 'assumption'). This is probably not worth belabouring, but our logic is as follows. The way the RDH model was constructed (by Bacon et al. 1991) assumed that patch dispersion and patch richness do not correlate. We stressed in our Oikos paper (Johnson et al. 2001a) that this assumption (that patch dispersion and patch richness are independent) ought to be empirically verified in the field. Nevertheless, given this theoretical assumption within the model, the RDH expects no relationship between GS and TS, which therefore constitutes a prediction. If there *is* a relationship between GS and TS, then the RDH can be rejected, which also constitutes a (very useful) prediction. The fact that other hypotheses also predict no relationship does nothing to discount its importance; many theories (in any discipline) have overlapping predictions. We think this prediction is well encapsulated in the simple formulation that: 'the RDH predicts that territory size should generally be independent of group size, because an individual needs to defend the same number of patches, and thus guarantee food, as would a group' (Johnson et al. 2000, p. 184). This makes it clear that they should be independent, in the absence of some more complex underlying process (e.g. that patch richness increases with dispersion).

But the more important point here that Revilla misses is the crucial significance of testing GS versus TS empirically. If these variables *are* related, then group size may simply be a function of resource abundance per unit area, i.e. 'territory quality'. Such a relationship could instantly eliminate the need to invoke any more complicated theory (such as the RDH) as a constraint on group size (providing dispersion and richness are also not correlated). Therefore, checking that GS and TS are not simply related in this way is a crucial first step to any study wishing to test the RDH further. This is true whether or not one wants to call it an 'assumption' or a 'prediction' (which is a separate discussion of little consequence).

In Johnson et al. (2001a), we specifically declared our intention to examine this 'null' hypotheses before bothering to go to all the extra effort of testing other RDH predictions. Thus, Revilla is mistaken in thinking that 'a lack of correlation between GS and TS gives no additional information on the validity of the RDH'. On the contrary, it is a crucial part of eliminating a suite of alternatives. The fact that GS and TS did not correlate implied that something more complicated was going on, and therefore validated testing the RDH in more detail, which we published thereafter (Johnson et al. 2001b).

### *Are Wytham Woods unusual?*

Studies from Wytham Woods are sometimes criticized because it is seen as an unusual and possibly special case. Consequently, another crucial significance of the Oikos paper (Johnson et al. 2001a) was to replicate large sample tests of these relationships over all the years of the study to eliminate the possibility that RDH-type explanations had gained predominance in the past because of one-off oddities found in particular years. However, GS was *never* related to TS, a very robust and consistent result. We could therefore, for the first time, rule out several viable alternatives for the whole study period.

We agree that the RDH need not be the whole explanation for sociality in badgers, or even for sociality in Wytham badgers. But we do suggest that our recent work in this study site and on this species provide highly cogent test cases given that (a) it was upon that species and study site that the original idea was formed (Kruuk 1978), (b) a number of similar one-off tests existed for comparison, (c) the population has been continuously studied and (d) few alternative explanations for their sociality have been vindicated (especially at this site). Building on the comparative approach of Kruuk and Parish (1982), we have recently tried to expand our thinking to explicitly make comparisons with other European populations (Johnson et al. 2002a). Indeed, we specifically pointed to such comparisons as more useful tests of theories of badger social behaviour, given the heavy bias among badger studies towards those in the UK (Stopka and Johnson 2000). Testing RDH predictions within a population where resources are always heterogeneous can only establish the RDH as a valid logical explanation, which cannot be rejected *for that locality*. To stand up as a predictive theory, tests must be conducted between localities or with manipulation experiments, where it is specifically the degree of heterogeneity itself that varies between data points, not merely the predicted responses of other variables when heterogeneity is a given.

### **Between-population empirical support**

Revilla's Fig. 1 shows a significant negative correlation between group size and territory size when the comparison is made *across populations*, which is what we also found previously (Woodroffe and Macdonald 1993, Johnson et al. 2000). We are not sure of Revilla's intention in displaying this information, but in fact, if anything, it supports the RDH. *Between* populations, or *between* species with comparable resource requirements, the RDH predicts groups size and territory size to be unrelated or, if anything, negatively related (Bacon et al. 1991).

### **Within-population empirical support**

Revilla notes the mixed evidence resulting from tests of the RDH (including much which supports it). We suggest that this inconclusiveness partly results from a lack of good tests (Johnson et al. 2002b). We claimed (Johnson et al. 2001a) that after von Schantz (1984) 'there have been no other serious published falsifications or objections to the hypothesis in the twenty years since its appearance' (p. 266). Revilla criticizes this statement because another paper of ours did not find clear evidence for RDH predictions (Johnson et al. 2001b). That is true, but it seems illogical to criticize an earlier paper for its assessment of current literature because it is superseded by a later one. Surely one has to allow for the chronology of events and results. The later paper (Johnson et al. 2001b) did much to self-critique our own methodology and to highlight important problems that need to be resolved in improved future studies. More importantly, however, our recent review finds numerous papers supporting the RDH concept, and very few against (Johnson et al. 2002b).

Revilla then cites Kruuk and Parish (1987) as evidence against the RDH, given that they found a reduction in TS with decreased food availability. We would contend that this is not a specific prediction of the RDH, since decreasing food should decrease GS but the effect on territory would depend on other factors (and is therefore unclear). Furthermore, although earthworm availability did decrease during the study period, badgers were able to switch to other food types and, more importantly, some food sources increased, including stores of barley which were fixed in space and available throughout most of the year (Kruuk and Parish 1987). As a result, it is unclear exactly whether the independent variable (overall food availability) really did constitute a decrease. In any case, Revilla's reading of the results are wrong: In fact, group size *did* decrease (though not significantly), and there was 'no overall trend in their [territories] mean size' (p. 362) both of which match predictions of the RDH. Thus, in the authors' own words, 'the evidence for changes in clan ranges and group sizes was not conclusive, but what there was supported the RDH' (Kruuk and Parish 1987, p. 362). The reason they found 'predictions based on the resource dispersion hypothesis to be only partly borne out,' arose from findings they perceived as violations of RDH assumptions, including: territory overlap; individual ranges smaller than the entire group territory; migration of males into neighbouring territories; and the fusion of neighbouring clans. None of these rule out the RDH (Johnson et al. 2002b), indeed one could expect any or all of them under given circumstances with or without the RDH (particularly given the usual complexity of social group life). But more important is Kruuk and Parish's (1987) conclusion that there was 'an almost qualitative change in the spatial

organization, perhaps caused by the change in food availability. If this were the case, one could speculate that under the observed conditions of food stress ... the badger social organization reverts to the basic mustelid pattern of solitary individuals, with females in more or less exclusive ranges, overlapped by single males' (p. 363). In such a case, the RDH may no longer be an appropriate model to apply (and therefore also inappropriate to reject as a general explanation).

### Does male expansionism contradict RDH?

Males indeed apparently do 'expand their range, in some cases to encompass additional females.' But this is far from consistent. For example, in Revilla's next sentence, he cites Frank Tuytten's work (Tuytten et al. 2000) and notes that, in that study, 'males are reluctant to recolonize vacated areas' (p. 7). Tuytten et al. found that it was females that occupied vacant territories, with males only joining them later (Tuytten et al. 2000). Kruuk and Parish (1987) also noted that males expand in some regions but not in others. Thus, the evidence is contradictory on why this occurs and apparently confounded by other variables. Given that Revilla has already misidentified the RDH as focusing solely on food resources, the evidence he cites leads him to claim that 'any hypothesis of territory formation based purely on the defence of food will, on its own, be doomed to failure because the factors affecting different types of individuals can differ substantially.' It is good then, that the RDH is not at all based 'purely on the defence of food.' The RDH has always acknowledged that various resource-types may be simultaneously important, and that other factors unrelated to food dispersion, such as predator pressure or alloparental care, may operate simultaneously to contribute to forming and/or maintaining sociality (Macdonald 1983a). It is certainly incorrect to assume that the RDH is mutually exclusive of other hypotheses for sociality. This explicit view can be traced to the beginnings of the hypothesis. For example, Macdonald (1983a, p. 379) wrote that: 'resource (particularly food) dispersion is fundamental to the spacing and structure of carnivore society in that it may set the limits to the group and territory sizes within which other combinations of selective pressures operate'. We have ourselves documented complex interactions of resources with other social constraints in which, for example, dominant red foxes monopolise gardens leaving pastures to subordinates (Macdonald 1980, 1983b), or where food alone sets a framework for focal pairs of crab-eating zorros within which very complicated social substructures persevered (Macdonald and Courtenay 1996).

### Misapplication of RDH in the Spanish study

Revilla cites his own study (Revilla and Palomares 2002) which claims to refute the RDH. Yet that whole study is irrelevant to the debate because, as he notes, 'the key-habitat holding the main food resource was not patchily distributed' (nor was prey patchy *within* that single habitat). It is therefore puzzling that they should have invoked the RDH as a potential model of social organization in the first place. If resources were *not* heterogeneous then the RDH was an entirely inappropriate model. It was presumably invoked because it was seen as a theory for badger sociality, whereas in fact it is a theory for sociality in heterogeneous environments (in any species). Tests to refute theories surely have to be conducted where they *could* operate. Otherwise one could concoct a suite of tests for a hypothesis on an inappropriate system and, when they undoubtedly fail, conclude that the theory was invalid. Theories must be tested against alternative theories where all are feasible. Finally, Revilla's conclusion in the light of the Spanish study was that 'RDH can not be considered as a universal mechanism'. It seems remarkable that anyone would suggest it (or any other model) was, even if that study had been an appropriate environment. In the Spanish study, territoriality is apparently determined by the 'richness of trophic resources for the female, and the females for the male' (Revilla and Palomares 2002, p. 509), which conforms to the typical mustelid pattern (Johnson et al. 2000). Moreover, variation in small family group sizes appears to depend on territory quality, which varies with seasonal fluctuations in food availability.

Revilla next characterises the RDH as 'only' providing 'a mechanism explaining why there may be enough food resources in one territory to maintain more than one individual (or more than a pair of primary animals'. And that this 'single relationship' has then been used to 'infer that it is *the* single necessary mechanism explaining group formation' (our italics). We strongly disagree with this characterisation. We have already stressed that the RDH is not-mutually exclusive of other mechanisms for group formation (or maintenance). But given that we have sometimes proposed that the RDH could be a particularly important such mechanism, we would certainly prefer to correct Revilla's statement to 'infer that it is, *potentially*, a single mechanism explaining group formation' (i.e. one of many possible). We feel the RDH's importance and applicability may be very wide indeed (and indeed that the principle has wide application in diverse aspects of ecology (Dwyer and Minnegal 1985, Barret-Lennard et al. 2001), but we certainly do not think it is *the* explanation for any or all species, environments, or situations.

## Revilla's conclusions reconsidered

Whether one wants to call a relationship between GS and TS an assumption or a prediction, we advise anyone interested in testing theories of social group size variation to test for this relationship (and ideally, although difficult, to explore the relationship between richness and dispersion) before invoking more complicated theories such as the RDH.

Resource surpluses can of course be produced by mechanisms other than the RDH. However, using careful methodology, the RDH has specific predictions that, in combination, can distinguish it from other hypotheses (Johnson et al. 2002b, Table 3). We also wish to stress the point that given the huge diversity of species to which RDH might apply, it is unhealthy to concentrate too much on badgers (or red foxes).

We agree with Revilla that it is indeed a mixture of resources (of different types) and other behavioural-ecological factors that influence social spacing behaviour. We specifically stated this in our Oikos paper: 'While RDH effects may be absent in many species, it remains a potential underlying influence on group size variation in many others, even if it is masked by much stronger selective pressures such as the need for cooperative hunting or predator defence' (Johnson et al. 2001a, p. 266).

Revilla suggests that there is much 'empirical evidence in conflict with the assumptions and predictions of the RDH'. Without wishing to dispute each one, many of these constitute confounded or invalid tests or suffer from very small sample sizes. But more importantly, the number of positive findings in support of the RDH significantly outnumber those against it (Johnson et al. 2002b). In any case, Peters' (1991) quote in our introduction reminds us not to expect any model to work in all cases. At the least, therefore, mixed evidence is encouragement to persevere.

We are intrigued by Revilla's 'integrative hypothesis' (Revilla and Palomares 2002). We already said that neither the RDH nor any other theory is likely to be an exclusive explanation for sociality. However, it remains unclear how a theory that is essentially a theory allowing for all other theories can offer useful predictive power, which can then be tested empirically. For a start, models need to be simplifications of reality, not an amalgamation of all of its complexity. We are also concerned that the predictions of the 'integrative hypothesis' in his Table 1 would be very hard to measure and/or test and, more importantly, do not distinguish it from other existing hypotheses. Nevertheless, we look forward to a refinement of the 'integrative hypothesis' that offers predictions that can be tested simultaneously with those of the RDH and other models. What we must certainly not do, however, is to reject the RDH without anyone ever having tested it properly. We have ourselves run into a number of problems in trying to do

so, but these are certainly not insurmountable. While we and others have been working to solve such problems and produce better and larger sample tests, it would be a pity if others remain intent on sentencing the RDH to oblivion without a decent trial.

Without any adequate experimental evidence to reject the RDH (even our own, the flaws of which we explicitly pointed out here and at the time), we defer our concluding sentiments for how do deal with challenging but intriguing models to the Greeks: 'I would not, says Socrates, be confident about everything I say about the argument: but one thing I would fight for to the end, both on word or deed if I were able – that if we believed we should try to find out what is not known, we should be better and braver and less idle than if we believed that what we do not know it is impossible to find out [so] that we need not even try' (Plato, *The Meno*).

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