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**Author for correspondence:**
Benjamin L. Allen
e-mail: benjamin.allen@daff.qld.gov.au

# Top-predator control-induced trophic cascades: an alternative hypothesis to the conclusion of Colman *et al.*

Benjamin L. Allen†

School of Agriculture and Food Sciences, The University of Queensland, Gatton, Queensland, Australia

Colman *et al.* (2014 *Proc. R. Soc. B* **281**, 20133094. (doi:10.1098/rspb.2013.3094)) recently argued that observed positive relationships between dingoes and small mammals were a result of top-down processes whereby lethal dingo control reduced dingoes and increased mesopredators and herbivores, which then suppressed small mammals. Here, I show that the prerequisite negative effects of dingo control on dingoes were not shown, and that the same positive relationships observed may simply represent well-known bottom-up processes whereby more generalist predators are found in places with more of their preferred prey. Identification of top-predator control-induced trophic cascades first requires demonstration of some actual effect of control on predators, typically possible only through manipulative experiments with the ability to identify cause and effect.

There is great interest in the roles that top predators might play in shaping terrestrial food webs [1]. A particularly popular idea is that the lethal control of top predators initiates trophic cascades that ultimately produce negative consequences for small (and often threatened) mammals and other prey. In accord with this idea, Colman *et al.* [2] recently claimed that the lethal control of Australian dingoes (*Canis lupus dingo* and hybrids) reduces dingo abundance, increases the abundance of sympatric mesopredators (i.e. red foxes, *Vulpes vulpes*) and herbivores (kangaroos and wallabies, e.g. *Macropus* spp.), which then places increased predation and competition pressure on small mammals. Colman *et al.* [2, p. 7] interpreted an observed overall positive dingo–small mammal relationship as 'evidence that ecological cascades induced by the lethal control of an apex predator can produce unintended shifts in the composition of species assemblages and vegetation structure'. In this brief comment, I show that an actual effect of lethal control on dingoes was not shown, and also that their correlative observations might be interpreted as equally strong evidence for alternative bottom-up processes entirely unrelated to dingo control.

Colman *et al.* [2] looked for dingo and fox footprints at 20 points (or sand plots) along a 10 km dirt road over three successive nights (total) in two treatments (dingo-baited and unbaited areas) at each of seven sites sampled once only and several months apart over a few years. Colman *et al.* [2, p. 2] report that 'dingo control had been undertaken at least once each year for the last 5 years' prior to their surveys, and that 'lethal control' represented either aerial baiting or ground baiting, sometimes supplemented with trapping at different sites. However, no data were presented on the type, timing or efficacy of lethal dingo control at any site.

The log response ratio (ln(baited/unbaited)) used by Colman *et al.* [2] in their analyses is likely to be heavily influenced by the timing of the survey in relation to the timing (and efficacy) of predator control. Ignoring (or pooling) the influence of different predator control practices has undermined similar studies [3], because these different predator control practices are known to vary widely in their effectiveness [4]. From the limited information presented in Colman *et al.* [2], it is therefore impossible to determine whether or not predators were sampled immediately after control or up to 12 months after control (which allows ample time for post-control reinvasion, a phenomenon common

†Present address: Robert Wicks Pest Animal Research Centre, Biosecurity Queensland, Toowoomba, Queensland 4350, Australia.

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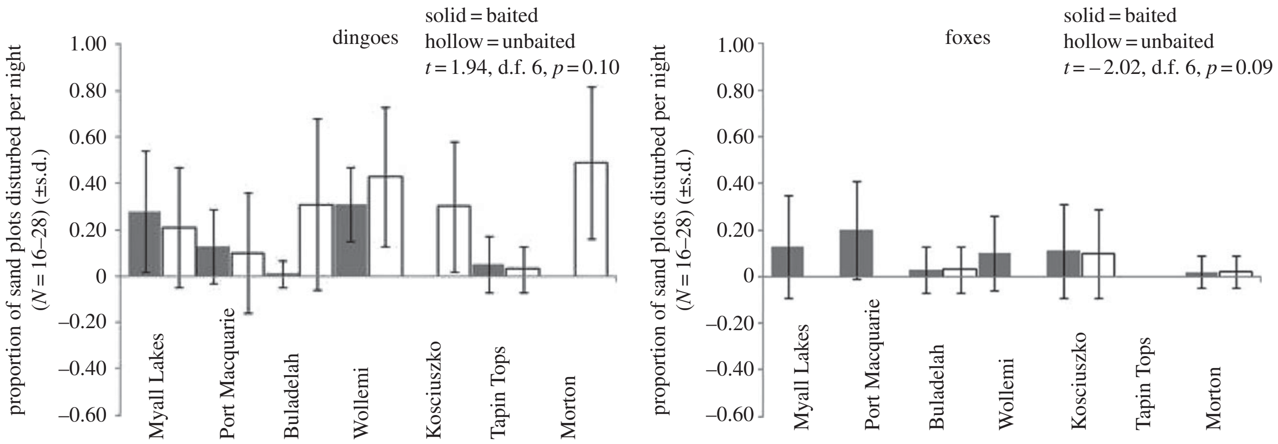


**Figure 1.** Dingo and fox activity in baited and unbaited areas at the seven sites surveyed by Colman *et al.* ([2]; adapted from their electronic supplementary material, table S1), including the results of a paired *t*-test for differences in mean predator activity between baited and unbaited areas.

for both dingoes and foxes; [4,5]). The extreme variability in the number of predators observed in baited and unbaited areas at different sites (figure 1) suggests 'time since control' and/or 'type of control' may have strongly influenced the data presented in Colman *et al.* [2]. Some sites (e.g. Morton or Kosciusko) obviously contribute disproportionately more weight to the assumed overall population 'reductions' than the other sites (figure 1). Thus, whether or not dingo control had any short-term and/or long-term numerical and/or functional effect on dingoes was completely unmeasured.

Demonstrating some actual effect of dingo control on dingo abundance and/or function is an indispensable prerequisite to claiming evidence for the trophic cascade presumed to follow (see [2], in chronological order, by [6–8]). At best, simple comparisons between area(s) A and area(s) B can demonstrate only a difference between the two; demonstrating a 'shift', 'change' or 'response' to baiting also requires at least a time 1 (pre-treatment) and time 2 (post-treatment) comparison [9,10], which was not attempted. Thus, no such effect was demonstrated, or is even possible from such snapshot data. Colman *et al.* [2] briefly acknowledge this caveat in their discussion, but ignore this caveat when formulating their published conclusion and later communicating their findings [11].

So how can the root data in figure 1 be subsequently handled in order to suggest 'evidence' for dingo control-induced trophic cascades? The answer lies in the *a priori* structural equation modelling (SEM) procedures used by Colman *et al.* [2], which focus strongly on top-down processes to the omission of well-known bottom-up processes. Thus, even ignoring the methodological shortcomings completely, there are equally if not more plausible alternative explanations for the results presented.

Colman *et al.* [2] interpret the positive dingo–small mammal relationship they identified as evidence for a complex dingo control-induced trophic cascade where dingoes ultimately provide protection to small mammals by suppressing mesopredators and macropods. However, the greater activity of dingoes in areas with greater activity of small mammals provides equally strong evidence for the more parsimonious interpretation that more dingoes are simply found in places with more of their prey. Dingoes are small generalist predators (mean adult body weight = 15 kg), and small- and medium-sized mammals (less than 15 kg) are favoured prey for dingoes in the region sampled by Colman and co-workers [12,13] and almost all other places in Australia as well [14,15]. Long-term studies on relationships between dingoes, mesopredators and their prey show that dingoes and mesopredators are positively correlated as they both synchronously fluctuate in response to bottom-up drivers of prey availability (see [16], which was not cited in Colman *et al.* [2] although Arthur and colleagues assessed 120 sand plots at the same time annually for 29 consecutive years in the very same study region). The difference between the results of the snapshot study of Colman *et al.* [2] and the 29 year study of Arthur *et al.* [16] may have something to do with their respective sampling efforts. That dingoes and other predators respond positively to bottom-up-driven increases in their preferred prey is well known [17–20]. Yet, this was not considered in the discussion or conclusion of Colman *et al.* [2] either, nor was its detection even possible in their results given that their *a priori* SEM did not permit prey species to positively influence dingo activity (fig. 3 in [2]). Colman *et al.* [2] advanced only the idea of top-down trophic cascades as explaining their observations even though bottom-up processes might also explain them. Identifying the actual causes (bottom-up and/or top-down) of simple correlations require manipulative experiments.

SEM appears to be an appropriate analytical approach for the type of snapshot data available in Colman *et al.* [2]. But to be useful, SEMs must properly account for known sources of variability and permit plausible alternative explanations that might not support a restricted set of popular *a priori* hypotheses [21]. The methodological weaknesses of Colman *et al.* [2] are not unique to that report, as poor application of otherwise robust methods and the disregard for plausible alternative hypotheses weaken most similar studies on this exact topic [22]. Although the publication of more quasi-experimental studies on dingoes and other predators is welcome, caution should be exercised against their ongoing interpretation as evidence for only top-down processes or evidence of dingo control-induced trophic cascades where an actual effect of dingo control on dingoes has not been demonstrated [23]. Such 'creeping cracks of bias' require correction and ought to be avoided [24] if ecologists hope to uncover the ecological truths waiting to be discovered.

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