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Evidence that dingoes limit abundance of a mesopredator in eastern Australian forests

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Summary

1. Aggressive behaviour of top predators may have strong effects on the distribution and abundance of mesopredator species. Such interactions between predator species can reduce the intensity of predation on vulnerable prey. Suppression of mesopredators by top predators is a potentially important process that could protect small prey species from unsustainable predation.

2. There is some evidence that in Australia, the dingo *Canis lupus* suppresses populations of the red fox *Vulpes vulpes*. This interaction could be significant to biodiversity conservation because while dingoes have been in Australia for several thousand years and coexist with a wide range of small mammals, the fox is a recent arrival which has caused declines and extinctions, and continues to threaten many prey species.

3. However the strength of the effect of dingoes on foxes is unclear, and some published data have been interpreted as demonstrating no relationship between abundance of the two species. These data come from forested habitats in eastern Australia, and may suggest that negative relationships of dingoes and foxes do not occur in complex habitats.

4. We re-analyse published data on fox vs. wild dog (i.e. dingoes plus, potentially, feral dogs and hybrids) abundance in eastern forests. These data reveal a triangular relationship of fox to wild dog density: when wild dogs are abundant, foxes are consistently rare, while when wild dogs are rare, foxes may be abundant but are not always so. This suggests that the abundance of wild dogs sets an upper limit on the abundance of foxes, but does not fully determine fox abundance.

5. Standard regression and correlation methods are not appropriate for analysing such triangular relationships. We apply two statistical methods that can be used to characterize the edges of data distributions, and use these to demonstrate a negative relationship of maximum fox abundance to the abundance of wild dogs.

6. *Synthesis and applications.* Our analysis adds to evidence that dingoes may have negative effects on red foxes in a wide range of habitats, and therefore, that dingoes may be significant to conservation of mammal biodiversity in Australia. It also illustrates problems and solutions in the statistical analysis of abundance of one species as a function of the abundance of another species with which it has a strong interaction.

Key words: mesopredator release, predation, dingo *Canis lupus dingo*, red fox *Vulpes vulpes*, quantile regression, analytical methods

Introduction

Interference competition between large mammalian predators can be a powerful factor limiting their distribution and abundance. In such competition, larger predators typically dominate smaller ones. Removal of large top predators can therefore result in population increase of smaller predators, in a process known as 'mesopredator release'. For example, wolves *Canis lupus* in North America limit populations of coyotes *C. latrans*, which in the absence of wolves increase in abundance (Berger & Gese 2007); in turn, coyotes suppress feral cats *Felis catus* and loss of coyotes allows cats to increase (Crooks & Soule 1999). Because mesopredators are typically versatile predators and can live at high population densities, mesopredator release can raise the total intensity of predation on smaller prey species (Courchamp 1999; Crooks & Soule 1999; Berger *et al.* 2008).

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Medium-sized Australian mammals have declined severely over the last 200 years, mainly because of predation by the red fox and feral cat (see review in Johnson 2006). Part of the reason for the extreme impact of these exotic mesopredators in Australia may be that much of the continent lacks larger predators able to impose top–down control on them. The one extant species that might fill this role is the dingo *C. lupus dingo*. The dingo arrived in Australia about 4000 years ago, replacing the thylacine *Thylacinus cynocephalus* and Tasmanian devil *Sarcophilus harrisii*, both of which went extinct on the mainland in the Late Holocene (Corbett 1995; Johnson & Wroe 2003; Johnson 2006). It occupied all habitats on mainland Australia but since the arrival of Europeans, its numbers have been controlled in many areas to protect livestock. Dingo abundance has been reduced over much of the continent, and the dingo has been all but eliminated from sheep-grazing areas in southern Australia.

There is evidence that dingoes do have strong effects on populations of red foxes and feral cats, providing protection for native mammals that are otherwise vulnerable to these mesopredators. Most of this evidence comes from arid and semi-arid habitats (Lundie-Jenkins *et al.* 1993; Smith & Quin 1996; Newsome *et al.* 2001; O'Neill 2002; Burrows *et al.* 2003; Southgate *et al.* 2007a,b; Johnson *et al.* 2007, Letnic 2007; Letnic *et al.* in press). However, other data suggest that the effect of dingoes on exotic mesopredators may be weak or inconsistent. In particular Catling & Burt (1995) found no significant correlations between dingo and fox abundance among sites in forest habitats in eastern New South Wales (NSW). Catling and Burt's results appear to conflict with other data published by Newsome (2001). Using similar survey methods to those of Catling and Burt, and working in similar habitats in south-eastern NSW, Newsome concluded that the abundances of dingoes and foxes were negatively related, but without providing a statistical analysis of his data. One interpretation of these apparently conflicting results is that effects of dingoes on mesopredators are greatest in open habitats, where mesopredators might find it most difficult to avoid dingoes, but are weak or non-existent in more complex forest habitats (Fleming *et al.* 2001; Mitchell & Banks 2005).

In this study, we re-examine the data of Newsome (2001) and Catling & Burt (1995) on abundance of dingoes versus foxes in NSW forests (the 'dingoes' recorded in both studies may well have included feral domestic dogs or dingo/feral dog hybrids, and for this reason, we hereafter refer to them by the more inclusive term 'wild dogs'). We point out that the original analysis of Catling & Burt (1995), using ordinary least squares correlation, was inappropriate to the structure of their data. A re-analysis of both the Catling and Burt (1995) and Newsome (2001) data sets shows a significant negative effect of wild dog abundance on fox abundance, that is consistent in both data sets. The key to our re-analysis is that we test whether the abundance of wild dogs placed an upper limit on fox abundance, rather than fully determining it. This mechanism would produce a triangular relationship of fox to wild dog abundance, rather than a simple linear

relationship. A relationship of this kind is best described by characterizing the edge of the scatter diagram, rather than fitting a central relationship through it (Blackburn *et al.* 1992; Scharf *et al.* 1998).

Our new analysis is significant to understanding of the way in which dingoes and foxes interact in Australia. More generally, the analytical approach illustrated here is likely to be appropriate to many other cases where researchers want to understand the relationships of abundance within pairs of strongly interacting species.

Materials and methods

Catling & Burt (1995) surveyed wild dogs, foxes, and other mammals in two large forested regions in eastern NSW: a southern region extending south–north from Bermagui (36°25′S, 150°04′E) to Ulladulla (35°22′S, 150°29′E), and a northern region from Port Macquarie (31°28′S, 152°25′E) to Grafton (29°40′S, 152°56′E); each region extended east–west from the coast to the top of the Great Dividing Range. Study areas in each region were selected to sample major eucalypt forest communities, with 13 in the south and 16 in the north. Abundances of wild dogs and foxes were indexed in each study area by recording presence or absence of tracks on sand plots placed on unsealed vehicle tracks. Sand plots were 1 m wide and extended from one side of the track to the other. Plots were placed at 200-m intervals along tracks, with between 10 and 35 plots per study area. Each plot was checked for animal tracks on three consecutive nights in late summer or autumn, and again in late winter or spring. The abundance index was calculated as the percentage of all plot-nights with tracks. Further details on study regions and methods are given in Catling & Burt (1995).

Newsome (2001) surveyed wild dogs and foxes in Kosciusko National Park and Nadgee Nature Reserve, in habitats broadly similar to those of Catling & Burt (1995) but to the west and south of their southern study region. Survey methods were similar, except that Newsome placed sand plots at approximately 1-km intervals. He did not detail plot size and number within study areas, or locations of study areas. Indices of wild dog and fox abundance were measured in a total of 15 study areas.

We re-analysed the data sets published by these authors, separately and for the combined data. Before combining the Catling & Burt (1995) and Newsome (2001) data sets, we transformed each abundance index by dividing by the maximum value for that data set, so that all values were standardized within a range from 0 to 1. This was done because differences in sampling protocols (such as plot size and spacing) could have introduced systematic differences into the raw values of abundance indices collected in the two studies. The range standardization would remove these differences, and would be valid provided that the range of true abundances indexed in the two data sets was similar. Given the environmental similarity and geographic proximity of the regions sampled in the two studies, this assumption is reasonable.

Results

The data of Catling & Burt (1995) and Newsome (2001) are shown in Fig. 1a and 1b. Catling and Burt calculated Pearson's correlation coefficients between fox and wild dog abundance and found no significant correlation in either of their study regions (south: $r = 0.38$; north: $r = -0.18$). The
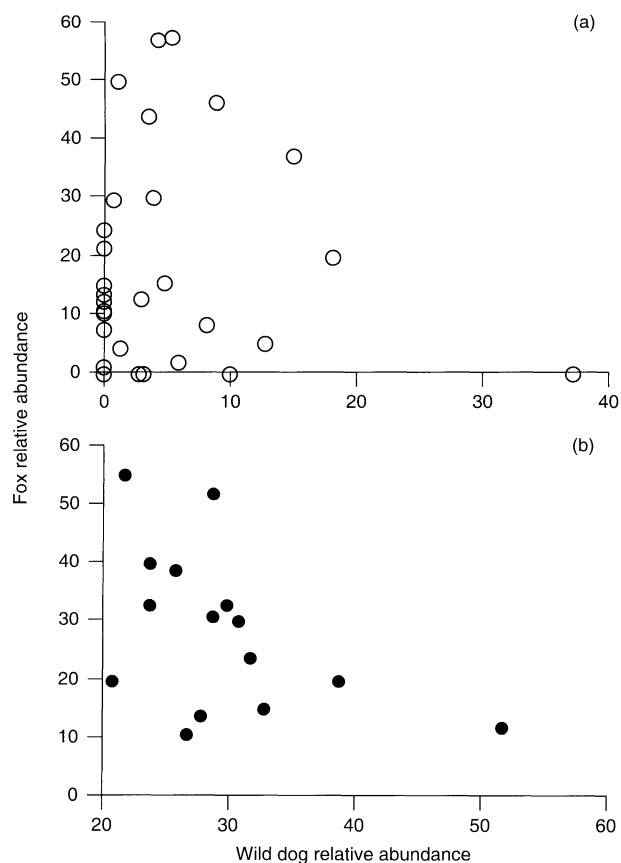
Fig. 1. Relationships between relative abundances of foxes and dingoes in forest sites across eastern New South Wales, data from (a) Catling & Burt (1995) and (b) Newsome (2001).

However, ordinary least squares (OLS) regression and correlation are not appropriate for these data, because these procedures assume that the variance of the y variable is uniform with respect to the value of the x variable. In both data sets, there is a clear tendency for the variance in y to decline with increasing x. This is especially obvious when the two data sets are combined (after range standardization). The scatter of points falls into a triangular space that fills the bottom-left part of the fox–wild dog plot (Fig. 2). OLS regression provides a poor description of the distribution of data (Fig. 2a). The pertinent statistical problem in a case such as this is to characterize and test the significance of the constraint line that defines the edge of the scatter of points, rather than to fit a line through the middle of the scatter. Two procedures for this have been discussed in the ecological literature.

First is quantile regression (Scharf *et al.* 1998; Cade *et al.* 1999). Quantile regression fits some quantile value of the distribution of the y variable as a function of the x variable. Fitting higher quantiles of y as a function of x should estimate the position of the edge of a triangular data scatter. Quantile regression is robust to outlying data values and skewed data distributions (Cade *et al.* 1999), so is appropriate for this data set.

Figure 2a shows the 0·9th quantile fitted to the fox/dingo data (significant at $P = 0·02$; regression calculated using the quantreg library (version 4·10) in the R statistical package version 2·5·1, http://www.R-project.org). Figure 2b shows the magnitude of the slope of the regression as a function of the quantile value, from the 0·5th (median regression) to the 0·9th quantile. The magnitude of the slope of each regression line is a measure of the size of the effect of wild dog abundance on fox abundance. This comparison shows that progressively stronger effects are revealed as successively higher quantiles are analysed up to the 0·9th (the slopes for all quantiles were negative). The 0·9th quantile best described the fox/wild dog data based on a goodness-of-fit measure for quantile regressions (Koenker & Machado 1999) (Fig. 2c; as traditional goodness-of-fit measures are not applicable to quantile

correlation across all their study areas is $r = -0·07$ ($P = 0·72$). Similarly, linear least squares regression finds no significant effect on fox abundance of wild dog abundance for the Catling and Burt data set (northern and southern regions combined). The same statistical analysis suggests that the correlation of wild dog and fox abundance was also non-significant in Newsome's (2001) data ($r = -0·47$, $P = 0·07$).
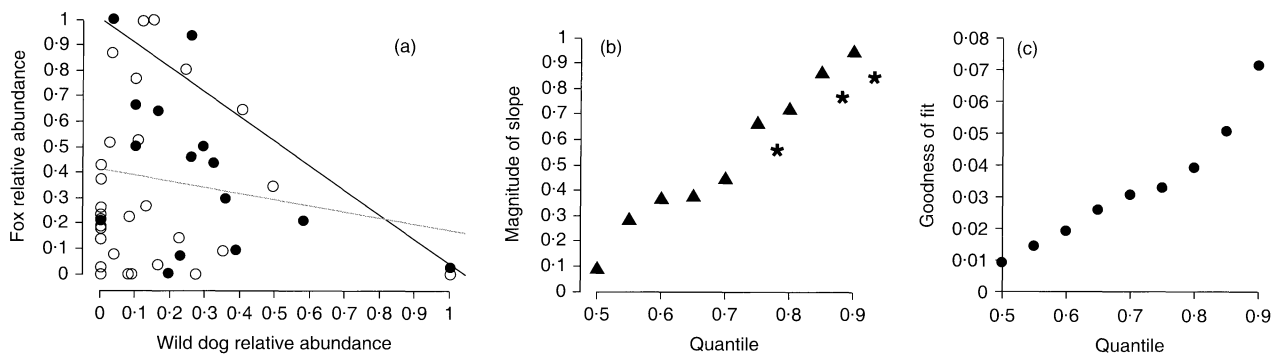

Fig. 2. (a) combined data of Newsome 2001 (filled circles) and Catling & Burt 1995 (open circles), showing the regression fitted to the 0·9th quantile of fox abundance (dark line, $P = 0·02$), and the regression fitted by ordinary least squares (pale line, n.s); (b) relationship between the quantile fitted and the magnitude of the slope of the regression (asterisks identify significant regressions); (c) relationship of the fitted quantile to Koenker & Machado's (1999) measure of goodness of fit of quantile regression. n.s, not significant.
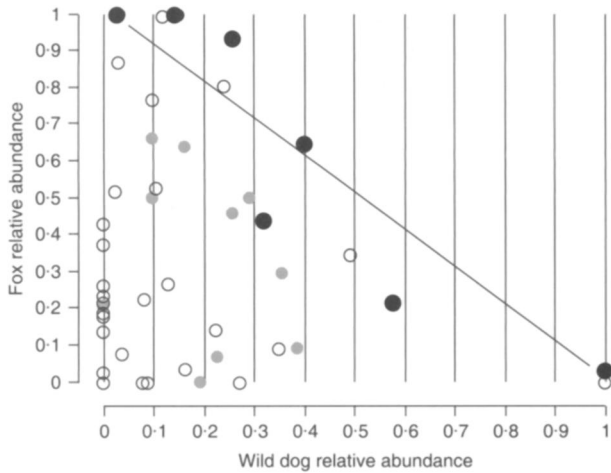
Fig. 3. The relationship of fox to wild dog abundance analysed using the method of Blackburn *et al.* (1992): dingo abundance is divided into 10 intervals of equal width, and the maximum fox abundance in each interval is highlighted. The relationship of maximum fox abundance to mid-point dingo abundance is significant ($F_{1,5} = 24 \cdot 08$, $r = -0 \cdot 92$, $P < 0 \cdot 005$).

regressions, the goodness-of-fit measure used here is a measure of local goodness-of-fit for a specific quantile, not a global measure of fit over the conditional distribution).

An alternative procedure for characterizing the edges of scatter diagrams was proposed by Blackburn *et al.* (1992). It consists of dividing the range of the *x* variable into discrete intervals, selecting the maximum *y* value for each interval, then using OLS to regress the maximum *y* values on the mid-point *x* values of each of those intervals. This is applied to the Newsome/Catling and Burt data set in Fig. 3, where wild dog abundance is divided into 10 intervals and the maximum fox abundance in each interval is identified. The OLS regression of y_{max} on *x* is significant ($F_{1,5} = 24 \cdot 08$, $r = -0 \cdot 92$, $P < 0 \cdot 005$). A problem is created, however, by the selection of extreme values within intervals: the probability that an extremely high value will occur in a sample increases with the size of the sample; where sample size varies systematically over the range of the *x* variable, this should produce a trend in the relationship of y_{max} to *x* (Scrivener *et al.* 2004).

In the present case, there are more sites with low wild dog abundance than with high wild dog abundance. The chance of finding very high values of fox abundance is correspondingly greater where wild dog abundance is low, simply because there are more such cases. This should generate a negative relationship between maximum fox abundance and wild dog abundance even when wild dog and fox abundance are actually independent of one another.

We evaluated this effect using a randomization. Values of wild dog abundance and fox abundance were randomly assigned to one another, and we then applied the Blackburn *et al.* (1992) procedure as described above to the randomized data and calculated the correlation (Pearson's *r*) of y_{max} and the mid-point value of *x*. This procedure was iterated 1000 times and the resulting distribution of values of *r* is shown in Fig. 4. The correlations were mostly negative, as expected, but the value of *r* calculated for the original data was $-0 \cdot 92$, which is more negative than 97·7% of the values calculated from the 1000 randomizations. This analysis therefore shows that, in spite of sampling artefacts, the negative relationship of maximum fox abundance to wild dog abundance is statistically significant.

The skewed distribution of data on wild dog abundance meant that there were only a small number of cases of high wild dog abundance matched with low fox abundance. We checked whether the evidence for a triangular relationship was due only to those few extreme cases by sequentially deleting the highest values and re-calculating the regressions using the procedure described above. This showed that the evidence for a triangular relationship was consistent across the full range of wild dog abundance (results not shown).

Discussion

Our results reveal a strong negative relationship between the abundance of wild dogs and foxes in forested environments of eastern Australia. The indications of a negative interaction between the two species are similar in the data of Catling & Burt (1995) and Newsome (2001), notwithstanding that these authors drew opposite conclusions from their respective studies. The triangular relationship that we demonstrate for
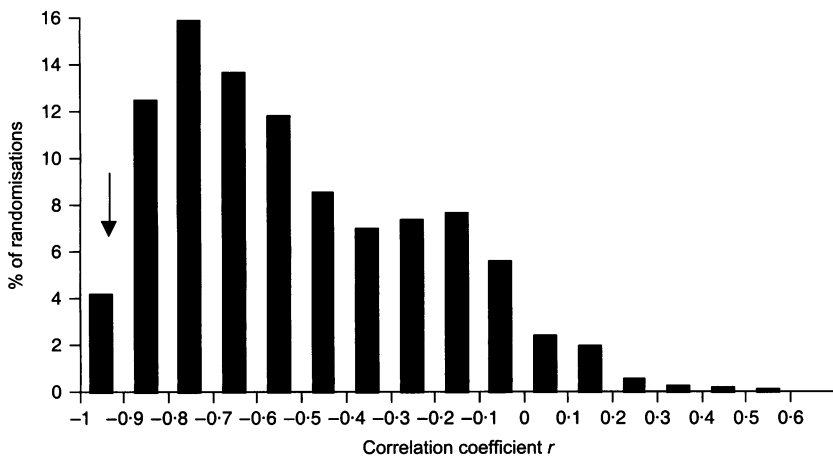

Fig. 4. Results of the Blackburn *et al.* (1992) technique applied to 1000 randomizations of the data in Fig 3, showing the distribution of values of *r* between maximum fox abundance and mid-point wild dog abundance. The *r* value for the original data is marked by the arrow.

these data are consistent with the idea that wild dog abundance sets an upper limit on the abundance that foxes can reach. When wild dogs are abundant, foxes are consistently rare or absent. When wild dogs are rare, foxes may be abundant, but are not always so; this may be because factors other than wild dogs also affect the abundance of foxes and may sometimes act to hold fox abundance low even when wild dogs are rare. There could be many such factors, but one that might be especially important here is poison baiting directed at wild dogs. Such baiting also affects foxes, and may account for many sites at which both species were rare.

We cannot be certain of the mechanism producing the negative correlation of abundance of these two predators. Direct limitation of foxes by wild dogs would appear to be a strong possibility, given that studies of other mammal predators show that direct attacks by the larger predator can have major demographic effects on the smaller (Palomares & Caro 1999). For example, Heldin *et al.* (2006) found that 50% of red fox mortality in a population in Sweden was due to attacks by the larger Eurasian lynx *Lynx lynx*. In cases such as these, an abundant large predator will easily enforce rarity on a smaller one. Indirect effects may also be important in controlling distribution and abundance of mesopredators, as smaller predators restrict their use of habitat to avoid encounters with their larger enemies. For example, avoidance of encounters with eagle owls *Bubo bubo* limited habitat use and breeding success of tawny owls *Strix aluco*, although actual attacks were rare (Sergio *et al.* 2007). The behavioural interactions of foxes and dingoes have been little studied, but there is some evidence that foxes avoid areas used by dingoes (O'Neill 2002; Mitchell & Banks 2005).

It is also possible that exploitation competition between the two species could be significant, given their extensive diet overlap (Mitchell & Banks 2005). Lastly, negative relationships could be due to different habitat preferences of the two species independent of any direct or indirect interaction between them. This is possible, but perhaps unlikely given the very broad habitat tolerances and geographic distributions in Australia of both species (dingoes occur in all habitats throughout mainland Australia, and red foxes occur throughout non-tropical parts of the continent).

Our re-analysis of the data of Catling & Burt (1995) and Newsome (2001) adds to evidence that negative relationships of dingo and fox abundance are common in Australia, and may be found in high-rainfall forested environments as well as in semi-arid and arid regions. Given the potential role of dingoes in reducing the impacts of fox predation on the biodiversity of small vertebrates in many parts of Australia (Glen *et al.* 2007; Johnson *et al.* 2007; Letnic *et al.* in press), it is crucial that the nature of the interaction between dingoes and foxes be better understood. Our study also emphasizes some of the pitfalls of analysing relationships of the abundance of strongly interacting species. Probably, triangular relationships are common in such cases. It is easy to imagine how interactions with a larger and more aggressive species might place a predator population under increasingly tight control as abundance of that dominant species increases; however, when released from top–down control by the dominant predator, abundance of the subordinate species would be free to vary over a wide range under the influence of many other factors. Ecologists studying effects of interactions between species on their abundance across different sites or times should therefore be wary of attempting to describe them with simple regression and correlation statistics.

Acknowledgement

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