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Research Letter

Does a Simple Cope's Rule Mechanism Overlook Predators?

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The Cope's rule predicts a tendency for species to evolve towards an increase in size. Recently, it has been suggested that such a tendency is due to the fact that large body sizes provide a general increase in individual fitness. Here we highlight evidence that predator species do not always fit the large-size = high-fitness mechanism for Cope's rule. Given the specific requirements of predators and the complexity of prey-predator relationships, any analysis that does not take into account all animal groups may overlook a significant portion of evolutive trends. Generalisations may not be possible regardless of taxa.

The Cope's rule [1] predicted, more than a century ago, a macroevolutionary tendency for species within a lineage to evolve towards an increase in size. Recently, Kingsolver and Pfennig [2] and Hone and Benton [3] suggested that such a tendency is due to the fact that large body sizes provide a general increase in individual fitness.

Without questioning the validity of the results presented by Kingsolver and Pfennig, or the convincing remarks of Hone and Benton, we would like to highlight evidence that predator species do not always fit the large-size = high-fitness mechanism for Cope's rule. Although Kingsolver and Pfennig presented several potential biases that could have occurred in the database they used for the review, they concluded that the generality of the pattern they observed was not an artefact of studying particular species. However, none of the 39 species included in Kingsolver and Pfennig's analysis was a mammalian or avian predator.

We consider that directional selection favouring larger size through fitness effects may be primarily a product of diet in predators. Predators are frequently strongly dependent on specific prey types, and hence face great pressures to adapt to stochastic or human-induced alterations of ecosystems. Moreover, complex prey-predator relationships can reverse the postulated positive correlations between size and either survival, mating success, or fecundity. We are conscious of the scarcity of information on size tendency in the evolutionary lineages of predator species, as well as on the relationships between their size and fitness, but we consider it important to point out two illustrative cases contrary to the pattern predicted by Cope's rule.

With a wingspan and a body weight that may attain more than 150 cm and 2500 g, respectively, the Eurasian Eagle Owl *Bubo bubo* is among the largest owls of the northern hemisphere and the largest owl ever to have lived [4]. But during the Middle Pleistocene (Mindel glaciation), eagle owls of southern France were 6–10% larger than recent individuals [*Bubo bubo davidi*; C. Mourer-Chauviré, PhD Thesis, University of Claude Bernard, Lyon, 1975] and a still larger *Bubo binagadensis* existed even later (upper Pleistocene) in the Caucasian province of Azerbaijan [4]. All of ancient, large *Bubo* owls seem to have been mammal hunters and the decline of the mammal fauna since the Tertiary has been considered the main cause of the size decrease of the Eurasian eagle owl's ancestors; moreover, it has been suggested that the present species may continue on this evolutionary trend of decreasing size [8].

Diet-associated size decrease in predator species is also evident as a current evolutionary phenomenon. Over recent decades, grouse populations in Finland showed an important human-induced decrease. Before this decrease, grouse represented the main prey of Finland goshawks, *Accipiter gentilis* (an avian predator with reversed-size dimorphism), for which the diet shifted toward smaller prey. As a consequence, sex-specific changes in morphology occurred. In particular, as a result of selective pressures due to changes in diet, males became smaller and females larger [5]. That is, because males provide most food from the beginning of breeding until fledging, small individuals may best be able to replace grouse with smaller birds and mammals. In contrast, because winter prey availability probably represents the most limiting factor for females (which do not hunt until late in the fledging period), an increase in female size may be beneficial for preying upon adult hares (much larger than grouse), the typical most profitable prey in their winter [5]. We (a work in preparation) recently detected that small size of individual male goshawks in a Swedish area with small preys was positively correlated with breeding performance (i.e., individual fitness): the smallest males fledged heavier males [GLM with nestling weight as a dependent variable-Poisson distribution, log link- and male-wing length (parameter estimate $\pm$SE $= -0.027 \pm 0.003$; $\chi^2 = 4.96$; $P = .026$) and territory in the rabbit-rich or poor area (parameter estimate $\pm$SE $= -0.070 \pm 0.036$; $\chi^2 = 6.42$; $P = .01$) as explanatory variables; intercept estimate $\pm$SE $= 15.398 \pm 1.113$% deviance explained = 37.1%]. Our results suggest that small males were most fit within the rabbit-poor area, where small individuals may be more efficient in replacing rabbits by hunting small- and medium-size birds, and shorter wings may facilitate them in pursuing birds within forest stands or close to woodland edges, typical hunting habitats of goshawks [6, 7].

Although Kingsolver and Pfennig convincingly showed the validity of the Cope's rule for plant and animal species other than predators, the examples above raise two other issues. First, we would add that a strong examination of predator species, originally or human-induced "restricted feeders," would also result in a more complete understanding of fitness-dependent lineage size evolution. Finally, we speculate that if lineage size evolution of predators is driven by changes in size of prey, the same may be true for herbivores, with Cope's rule mainly an effect of selection on plants to outgrow the reach of herbivores. Given the specific requirements of predators and the complexity of prey-predator relationships, any analysis that does not tally all animal groups may overlook a significant portion of evolutive trends. For this reason, the scarce information available on predator evolutionary patterns indicates that generalisations are not always possible and, above all, they may not be possible regardless of taxa.

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