

Is absence of proof a proof of absence? Comments on commensalism

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ARTICLE INFO

Article history:

Received 13 October 2010

Received in revised form 16 January 2011

Accepted 18 January 2011

Available online 25 January 2011

Keywords:

Commensalism

Parasitism

Mutualism

Fossil record

Null hypothesis in palaeoecology

ABSTRACT

Commensalism in the narrow sense can be understood as an interaction strictly neutral for one organism and positive for the other. Neutral interaction is the absence of interaction and as such it cannot be proven (the proof of absence cannot be made) and consequently it can be regarded as a concept unfit for empirical science. In the broad sense it is often understood as a weak (positive or negative) interaction on one hand and positive on the other. This approach also seems imperfect, as weak interactions should be regarded rather as mutualism or parasitism, respectively. The borders between interactions (commensalism/parasitism and commensalism/mutualism) are difficult to define; hence commensalism should rather be considered as a theoretical interval within the continuum of interactions. Detection of commensalism in recent associations is rather difficult, while in the fossil record it seems impossible. Commensalism as a null hypothesis in paleoecology cannot be retained, as the possibility of making a type II error is very high. The terms “paroecia” and “endoecia” seem to be more useful to use in cases when a particular ecological relationship is difficult to prove.

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1. Introduction

Commensalism has often been implicitly treated as a null hypothesis in ecology and paleoecology. Biologists can observe living animals with direct live recording of interactions among them; in paleoecology, however, the inconvenient reality is that most of the interactions are lost during taphonomic processes (Tapanila, 2008). The applications of concepts developed by ecology into paleoecology should therefore be taken with care. In the majority of cases interactions between two organisms are not obvious and more developed studies need to be undertaken to recognize them (e. g. Gahn and Baumiller, 2003; Zapalski, 2005). Commensalism has been postulated by numerous authors, and is very often recognized in the fossil record (most recent papers are by de Gibert et al., 2006; Wisshak and Neumann 2006; Ishikawa and Kase, 2007; Zhan and Vinn, 2007; Rodrigues et al., 2008; Martinell and Domènech, 2009; Môtus and Vinn, 2009; Odin, 2009). Other interactions such as parasitism or mutualism are seldom reported (e. g. Bates and Loydell, 2000; Bassett et al., 2004; Neumann and Wisshak, 2006; Zapalski, 2007; Zapalski and Hubert, 2011; Klug et al., 2011 see also Conway Morris, 1981). Predation, also very commonly recognized interaction in the fossil record (e. g. Ebbestad et al., 2009; Klomp maker et al., 2009; Lindström and Peel, 2010) is not taken into account in this analysis, because it does not involve long coexistence of two organisms; this analysis concerns only symbiotic (*sensu lato*) relationships.

It will be shown here that commensalism is nearly impossible to detect in recent associations (due to biological and philosophical premises). Even if it be possible, it has been shown that organisms being temporarily commensal may become parasites or mutualists under the influence of various environmental factors and the character of this relationship can change during the life of individuals. Finally, commensalism has been proposed as a null hypothesis in paleoecology (Tapanila, 2008); it will be shown that this is difficult to follow.

2. Classification of interactions

One of several possible classifications of interactions uses the effect of the interaction as a criterion (Lewis, 1985). It can be positive (+), negative (−) or neutral (0) for each organism involved in the relation (Odum and Barrett, 2005; Dobson et al., 2008). The most commonly occurring interactions (such as mutualism or parasitism) require positive or negative effects on each involved organism. Such effects can be of varied intensity – for example a negative effect of the parasite can be expressed as an indistinct illness of the host at one end, and by the host's death at the other. It can be shown on the number line (Fig. 1) that the intensity of a positive interaction can be expressed as $(0; \infty)$, and the range of a negative interaction as $(-\infty; 0)$, both excluding zero. The neutral interaction requires a single value, namely 0. A similar presentation was given by Darell and Taylor (1993).

In other words, let any two objects be given; interactions between them can be negative, neutral or positive. We have therefore three sets of interactions; positive and negative interactions are continuous

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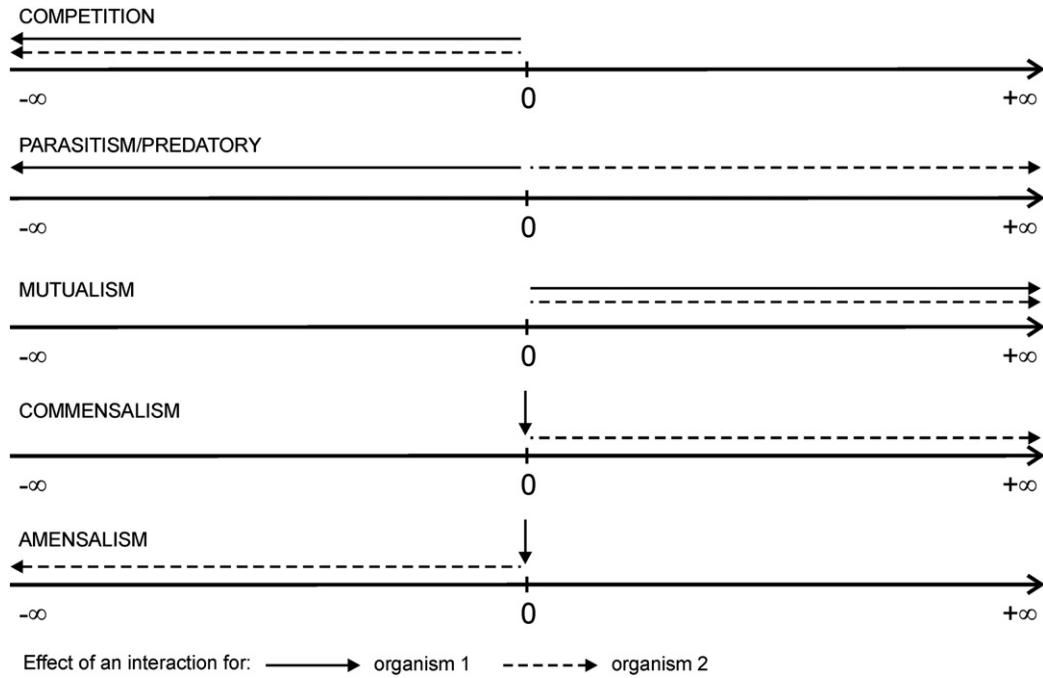


Fig. 1. Ecological interactions and their effects on involved organisms, expressed on number lines.

and have their magnitude, while neutral interaction has only “0” value. Thus we have positive and negative interactions with broad number of possible values, and neutral interaction with only one possible value.

3. How frequent are interspecific interactions?

The probability of finding an element from one of the two large sets is greater than finding the element from a remaining single-value (or single-element) set. Even if all values are not equally probable to occur, we can argue for negative and positive interactions being more common than neutral interaction. Hence, parasitism and mutualism should be recognized much more often than neutral interactions.

Having a look at the ISI Web of Knowledge browser it can be found that browsing for “parasit*”, the site returns more than 90 thousand documents; for “mutual*” – more than 40 thousand; finally, for “commensal*” – less than 4 thousand. Most of these papers concern recently living organisms. The latter interaction occurs in this database at an order of magnitude less often than the two former ones. Of course, the database covers various kinds of articles (showing that an organism is not a parasite, for example), but nonetheless gives a general idea as to how often the given interaction is under research – and with some approximation, in consequence – how often it occurs in nature. To support these considerations it can be stated that parasites dominate the ecosystems – some researchers suggest that most of species on Earth are parasites (Windsor, 1998); 75% of links in natural food webs probably involve parasites (Lafferty et al., 2006; Dobson et al., 2008). It can be added that a healthy ecosystem is rich in parasites (Hudson et al., 2006).

The fossil record is strongly biased in the terms of biodiversity and anatomy. It can be presumed that ecological relations in the fossil record are biased as well. Surprisingly, out of all symbiotic relationships commensalism is incomparably more often recognized in fossil record than other symbiotic relationships (e. g. Schneider, 2003; Ishikawa and Kase, 2007; Zhan and Vinn, 2007; Tapanila and Ebbestad, 2008; Odin, 2009; Key et al., 2010).

4. Commensalism – biological perspective

Papers describing commensalism in modern associations usually argue for it in two ways. The first is simply to assume that if large numbers of symbionts are tolerated by the host, then that means that they are harmless (e. g. Browne and Kingsford, 2005; Dvoretzky and Dvoretzky, 2009). The other way of arguing states that there is very little cost to the host (e. g. Goto et al., 2007; Lee et al., 2009). There are many papers which simply assume commensalism without discussing it (e. g. Steele et al., 1986; Parente and Hendrickx, 2000; Thomas and Klebba, 2007; Kane et al., 2008). Very rare papers state argument for positive effect on one hand and state inability of detecting positive or negative effect on the other – and therefore assuming neutral effect (e. g. Mosher and Watling, 2009).

The first argument can be easily rejected by comparison with parasites. Well established parasites are not greatly harmful to the host, the most harmful parasites are usually these having very short common history with their host. Tolerance of parasites is very common in recent host–parasite associations (Miller et al., 2005). Well fit parasites can be tolerated by their hosts even in very large quantities – for example red foxes in Southern Poland are commonly infested by a tapeworm *Echinococcus multilocularis* – about 86% of the host individuals possess 1–100 parasites, but about 4% have more than 1000 tapeworms (Borecka et al., 2008; see also data on parasite infection in wolves given by Kloch et al., 2005). These tapeworms are undoubtedly tolerated by the host, especially at low infestation rates. And they are undoubtedly parasites (e. g. Gottstein and Hemphill, 2008; Bagrade et al., 2009). Therefore the argument on toleration of high infestation does not support the conclusion on commensalism. Moreover, in the present author's opinion it is methodologically wrong when an interaction is analyzed between the host and endobionts *en masse* – while the interaction occurs between two individuals, a host and a symbiont.

In the quoted example of red foxes (Borecka et al., 2008) it can be imagined that a small number of “commensals” make “very little cost” to the host; at very high infestation rates they “become” parasites, which are really harmful to the host. There is a common argument on

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