Interspecific aggressive behaviour in salamanders: species-specific interference or misidentification?

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Abstract. This research analyses variation in the interspecific aggressive behaviour of two salamander species, *Plethodon jordani* and *P. glutinosus*, from three localities which differ in extent of sympatry, the intensity of interspecific competition and frequency of hybridization. If interspecific aggression evolved by misidentification of species, it should either (1) vary concordantly with the frequency of hybridization, or (2) be similar in all of the localities. If selection for interspecific interference has occurred, interspecific aggression should vary concordantly with interspecific competition. Misidentification can account for variation in the interspecific aggressive behaviour of *P. glutinosus*. *P. glutinosus* from all localities did not distinguish behaviourally between heterospecifics and conspecifics. In contrast, for *P. jordani*, results suggest that alpha-selection has occurred under conditions of strong interspecific competition. *P. jordani* from the locality where interspecific competition is weak were less aggressive to heterospecifics than to conspecifics, while *P. jordani* from two localities where interspecific competition is strong were equally aggressive to heterospecifics and conspecifics.

Many intraspecifically territorial animals are known to exhibit aggressive behaviour toward members of other species (Orians & Willson 1964; Cody 1969; Murray 1981). The widespread occurrence of interspecific aggression suggests that it has evolved in many contexts and serves a variety of biological roles. One obvious role is the exclusion of competitors from a local supply of limited resources (Howard 1913); another, less obvious, role is the reduction of nest predation (Dunn 1977).

While interspecific aggression requires an investment of time and energy (Brown 1964), it may confer a net benefit to individuals that exhibit it, at least in some cases (Morse 1980). In the context of current benefit, the adaptiveness (Bock 1980) of interspecific aggression is not controversial.

However, several authors (e.g. Williams 1966; Gould & Lewontin 1979) claim that current benefit alone is not a sufficient criterion of adaptation. In order to distinguish adaptations from fortuitous effects (Williams 1966) (or adaptations from 'exaptations', Gould & Vrba 1982), it is necessary to demonstrate that a feature has been subjected to natural selection specifically for the biological role that it now performs. Gould & Vrba (1982) point out that such demonstrations are always difficult,

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and often impossible. Thus, it is inevitable that the list of beneficial features will be longer than the list of adaptations, and many features that are indeed adaptations will never be identified as such. However, in this light, cases that are amenable to historical analyis of selection pressures should be of special scientific interest. The evolution of interspecific aggression in the terrestrial salamanders *Plethodon jordani* and *P. glutinosus* is one such case.

To demonstrate that interspecific aggression is an adaptation, one needs to find evidence that it has been influenced by natural selection for interspecific interference per se, rather than by natural selection for intraspecific aggression.

Under the 'misidentification theory' (Tinbergen 1935, 1936; Lorenz 1966), intraspecific aggression is an adaptation for reducing the local impact of conspecific competitors, and aggression is directed toward heterospecific individuals fortuitously, because of their apparent similarity to conspecifics. Interspecific aggression resulting from misidentification is non-adaptive because selection pressures on intraspecific aggression are responsible for the origin and maintenance of heterospecific aggression in the population. Support for the misidentification theory has come from observations that the intensity of aggression elicited by heterospecifics (Murray 1969, 1981; Rasa 1969; Kohda 1981) or the reaction distance to heterospecifics (Moran &

Sale 1977) depends on the morphological similarity between heterospecifics and conspecifics.

Because morphologically similar species are likely to be similar ecologically, they are also likely to be competitors. When morphologically similar species are ecological competitors, interspecific aggression arising from misidentification may be beneficial (Murray 1981). In this case interspecific aggression is exaptive, not adaptive (contra Murray 1981).

Interspecific aggression may also arise as an interference mechanism in response to conditions of interspecific competition. This process has been called alpha-selection (Gill 1974). Under alpha-selection, interspecific aggression is species-specific, and is independent of selection for intraspecific aggression. Support for an independent origin of interspecific aggression has come, for instance, from the observation that aggression toward novel species develops only when those species utilize the same food resources (Losey 1981, 1983).

The present study was undertaken to determine whether interspecific aggressive behaviour has evolved by misidentification or by alpha-selection in two species of terrestrial salamanders, *P. jordani* and *P. glutinosus*. These salamanders are ideal subjects for evolutionary studies because they exhibit significant variation in interspecific ecological and behavioural interactions among localities (Hairston 1949, 1950, 1951; Highton & Henry 1970a; Highton 1972; Nishikawa 1985a). Here, I analyse the pattern of variation in the species specificity of aggressive behaviour among *P. jordani* and *P. glutinosus* from three localities in the southern Appalachian Mountains (Fig. 1) in which the ecological and behavioural interactions between the two species are different.

GEOGRAPHIC VARIATION IN ECOLOGICAL INTERACTIONS

P. jordani and *P. glutinosus* are morphologically and ecologically similar. Both species are active above ground from May to October at intermediate elevations in the southern Appalachians (Hairston 1949, 1950; Highton 1962a), courtship occurs from July to October and females lay eggs underground the following May (Highton 1962b; Hairston 1983a). Both species occupy exclusive territories on the forest floor (Nishikawa 1985b), and feed nocturnally on a wide variety of inverte-
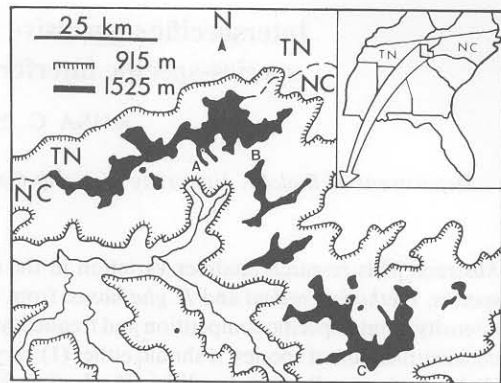
Figure 1. Map of the Great Smoky and Balsam Mountains in North Carolina (NC) and Tennessee (TN), showing the study areas. Black areas are above 1525 m. The 915 m contour is shown by the hatched line. A = Kephart Prong, B = Heintooga, C = Courthouse Creek.

brates (Hairston 1949; Powders & Tietjen 1974). The larger species, *P. glutinosus*, occupies smaller and more exclusive territories than *P. jordani* (Nishikawa 1985b).

In the southern Appalachian Mountains, several geographic races of *P. jordani* occur in at least 22 high elevation populations, and several cryptic species of the *P. glutinosus* complex occur in the intervening lowlands (Highton & Henry 1970a; Highton 1972, 1983; Highton & MacGregor 1983). Each population of *P. jordani* is sympatric with a member of the *P. glutinosus* complex at intermediate elevations (Hairston 1949, 1951, 1980a, b). At all of the localities included in this study, only one species of the *P. glutinosus* complex, *P. teyahalee*, is found. I have retained the name *P. glutinosus* here because it is used in all of the previous literature on interspecific interactions between these salamanders throughout the southern Appalachian Mountains.

The extent of sympatry, the intensity of interspecific competition, the frequency of hybridization and the intensity of interspecific aggression between *P. jordani* and *P. glutinosus* vary among localities (Hairston 1949, 1951, 1980a,b; Highton & Henry 1970a; Highton 1972; Nishikawa 1985a).

At Courthouse Creek (Fig. 1) in the Balsam Mountains, *P. jordani* and *P. glutinosus* are broadly sympatric over a vertical range of more than 1200 m (Hairston 1949, 1951, 1980a; Highton & Henry 1970a; Highton 1972); intraspecific competition is

more intense than interspecific competition for both species (Hairston 1980a); and hybrids have not been found despite extensive ecological and electrophoretic studies (Hairston 1951, 1980a; Highton & Henry 1970a,b; Highton 1972).

In the northeastern Great Smoky Mountains (hereafter referred to as the Smoky Mountains or Smokies), the species are narrowly sympatric over a vertical range of only 70–100 m (Hairston 1951, 1980a; Highton & Henry 1970a); interspecific competition (relative to intraspecific competition) is more intense here than in the Balsam Mountains (Hairston 1980a,b).

The frequency of hybridization varies within the Smoky Mountains (Highton 1972). On Heintooga Ridge (Fig. 1), 5–15% of adults are hybrids (Hairston, personal communication; personal observation), but hybrids have not been found along Kephart Prong on Richland Mountain (Fig. 1), 10 km west of Heintooga (Highton & Henry 1970b). Hairston (1980b) found hybrids at very low frequencies (< 0·001) at Taywa Creek on Hughes Ridge, midway between Heintooga and Kephart Prong. Table I summarizes the ecological interactions between species at each locality.

PREDICTIONS OF THE THEORIES

Because of the variability in interactions between *P. jordani* and *P. glutinosus*, it is possible to determine whether misidentification or alpha-selection best explains the evolution of interspecific

aggressive behaviour in these species. The method employed was first to determine the intensity of interspecific aggression relative to the intensity of intraspecific aggression in each area, and then to compare the observed pattern of variation in the relative intensity of interspecific aggression to the patterns of variation that are expected if misidentification or alpha-selection has occurred.

If alpha-selection has occurred under conditions of interspecific competition, then the intensity of interspecific aggression (relative to intraspecific aggression) should vary concordantly with the intensity of interspecific competition (relative to the intensity of intraspecific competition). Salamanders of both species from localities where interspecific competition is intense (i.e. Heintooga and Kephart Prong) are predicted to be relatively more aggressive to heterospecifics than salamanders from the locality where competition is less intense (i.e. Courthouse Creek). This prediction requires the assumption that the intensity of interspecific competition at Heintooga and Kephart Prong is the same as it is on Hughes Ridge, where it was originally measured by Hairston (1980a,b). The assumption is reasonable because Heintooga and Kephart Prong are less than 10 km from Hughes Ridge, and are similar to Hughes Ridge in the vertical extent of sympatry (Highton & Henry 1970a; Hairston 1980a).

If interspecific aggression has arisen by misidentification, as a fortuitous consequence of selection for intraspecific aggression, then the intensity of interspecific aggression should vary concordantly

Table I. Summary of ecological interactions between *P. jordani* and *P. glutinosus* at three localities in the southern Appalachian Mountains

Locality	Vertical extent of sympatry	Competition coefficients‡		Frequency of hybrids
		$\alpha_{j,g}$	$\alpha_{g,j}$	
Heintooga	70–100 m*	(2·25)	(0·19)	5–15%
Kephart Prong	70–100 m†	(2·25)	(0·19)	0%†
Courthouse Creek	> 1200 m*	0·63	0·14	0%*

* From Hairston (1980a,b).

† From Highton & Henry (1970a,b).

‡ Lotka–Volterra competition coefficients were estimated by Hairston (1980a) from the numerical response of each species to removal of heterospecifics over a 5-year period. Coefficients in parentheses were measured at Taywa Creek and are assumed to be similar at these nearby localities (see text).

with the intensity of intraspecific aggression. Because the absolute intensity of intraspecific aggression does not vary among the localities (Nishikawa 1985a,b), the relative intensity of interspecific aggression should be similar in all areas. This prediction requires the assumption that salamanders from all localities are equally able (or unable) to perceive differences between conspecifics and heterospecifics.

Because the frequency of hybrids varies among the localities, it is possible that species recognition may also be variable. Thus, a plausible alternative prediction of misidentification is that the relative intensity of interspecific aggression will vary concordantly with the frequency of hybridization. This prediction requires the assumption that reproductive misidentification and aggressive misidentification have a common causal basis. Under this assumption, the misidentification theory predicts that salamanders should be less aggressive to heterospecifics (relative to conspecifics) in the localities where hybridization does not occur (i.e. Courthouse Creek and Kephart Prong) than in the locality where hybridization is more frequent (i.e. Heintooga).

Analysis of variation in the absolute intensity of interspecific aggression is not sufficient to reject the misidentification hypothesis because of the requirement that inter- and intraspecific aggression should vary non-concordantly among localities. Thus, it was necessary to determine the intensity of interspecific aggression relative to the intensity of intraspecific aggression in each locality. When the intensity of interspecific aggression relative to the intensity of intraspecific aggression is compared among the localities, only the relevant non-concordant variation is included in the analysis. Also, because interspecific competition was measured relative to the intensity of intraspecific competition, the competition coefficients represent only the variation in interspecific competition that is not concordant with variation in intraspecific competition in each area. Thus, possible variation in the intensity of intraspecific competition among localities does not confound the analysis.

METHODS

Adult males and females of *P. jordani* and *P. glutinosus* were collected from three localities (Fig. 1). In the Balsam Mountains, salamanders were collected within 1 km of Hairston's (1980a,b) study site along Courthouse Creek, Pisgah National Forest, Transylvania County, North Carolina, U.S.A. (35° 16′22″N, 82° 53′20″W). Salamanders were collected from two localities in Great Smoky Mountains National Park, Swain County, North Carolina, approximately 50 km northwest of the Balsams study site: (1) on Heintooga Ridge along the Heintooga–Roundbottom Road (35° 37′30″N, 83° 10′22″W) approximately 8 km east of Hairston's (1980a,b) study site (i.e. along Taywa Creek on Hughes Ridge: this site was made inaccessible when a park road was closed in 1978); and (2) along Kephart Prong on Richland Mountain approximately 3 km from U.S. Route 441 (35° 36′13″N, 83° 23′21″W).

Salamanders from Courthouse Creek and Heintooga were collected between 11 May and 25 August 1982, and behavioural observations were made from 17 May to 2 December 1982. Kephart Prong salamanders were collected on 16 August 1983, and observations were made from 14 November 1983 to 20 February 1984. The salamanders from Kephart Prong were kept in captivity 100 days longer, on average, than salamanders from the other two areas. Time in captivity was not significantly correlated with the frequencies of aggressive behaviour patterns for either species in either type of encounter (*P. glutinosus*, $N = 33$, conspecific encounters, $r = -0.060$, heterospecific encounters, $r = -0.086$; *P. jordani*, $N = 39$, conspecific encounters, $r = 0.058$, heterospecific encounters, $r = 0.026$). However, other possible effects of this difference are discussed below.

All salamanders were kept in the laboratory at 15–18°C on a 12 h L:12 h D photoperiod. Each salamander was placed alone in a covered plastic dish (18·5 cm in diameter, 8 cm high) lined with wet filter paper, and was fed 50–75 *Drosophila melanogaster* once a week. Virtually all of the salamanders from both species gained weight during the experiment. Residents were allowed to habituate to laboratory conditions in their chambers for at least 3 days before the first observation. Each resident was fed 25–30 *D. melanogaster* 48 h before each encounter in order to control the level of satiation. All encounters took place within the chamber of the resident. Encounters were initiated by inverting the chamber of an intruder over the chamber of a resident, so that neither salamander was handled before testing. At the beginning of each observa-

tion, in order to simulate natural nocturnal foraging conditions, 25–30 *D. melanogaster* were added to the resident's chamber. Observations lasted 45 min and were made under dim, broad-spectrum red light, at least 0·5 h after the initiation of the dark phase of the photoperiod.

Fifteen *P. jordani* and nine *P. glutinosus* from Heintooga, 13 *P. jordani* and 12 *P. glutinosus* from Kephart Prong, and 11 *P. jordani* and 12 *P. glutinosus* from Courthouse Creek were observed during encounters with a heterospecific and with a conspecific intruder. Intruders were presented in random sequence at intervals of not less than 2 days. Each resident was observed only once in each type of encounter, but the same individual was occasionally used more than once as an intruder. Only the behaviour of residents is reported here. However, the behaviour of intruders was recorded: for both species, the frequencies of 11 aggressive and non-aggressive behaviour patterns exhibited by intruders did not differ significantly among localities more frequently than expected by chance alone (i.e. about 5% of the statistical tests were significant, unpublished data). Thus, geographic differences in intruder behaviour cannot explain the observed variation in the behaviour of residents that is reported in this study.

Only encounters between sympatric adult salamanders of the same sex were analysed; sex and reproductive state were confirmed by dissection after observation. Data for male and female residents were pooled because separate analyses yielded the same result as the pooled analysis.

Residents and intruders were paired at random with respect to body size. Neither the mean body weight of residents nor the mean difference in body weight between resident and intruder differed significantly among the samples of *P. jordani* or *P. glutinosus* from the three localities (*t*-tests, $P > 0.05$). In all heterospecific encounters, *P. glutinosus* was larger than *P. jordani*.

During encounters, the frequencies of four aggressive behaviour patterns were recorded for the resident salamander. The agonistic behaviour patterns of *P. jordani* and *P. glutinosus* (similar to those described for *P. cinereus* by Jaeger 1981, 1984) are as follows.

(1) Snap: a salamander opens its jaws and snaps them shut, which sometimes produces an audible sound.

(2) Lunge: a salamander moves rapidly in the direction of an intruder, but stops before making contact.

(3) Chase: a salamander follows directly the path of a retreating intruder.

(4) Bite: a salamander contacts an intruder with its mouth, which sometimes causes injuries such as skin lacerations or the loss of up to 25% of the tail.

There were no significant differences in the frequencies of five non-aggressive behaviour patterns between conspecific and heterospecific encounters for either species from any of the localities (Wilcoxon tests, $P > 0.05$), so the data are not reported here.

For each species, the individual frequencies of each aggressive behaviour pattern and the total number of aggressive acts performed by a salamander during a heterospecific and a conspecific encounter were compared using the Wilcoxon matched-pairs signed-ranks test.

RESULTS

For *P. jordani* from Courthouse Creek, the frequencies of snap, chase and bite were significantly higher during conspecific encounters than during heterospecific encounters, and the total number of aggressive acts per encounter was also significantly higher during conspecific encounters (Table II).

For *P. jordani* from Heintooga, only the frequency of snap was significantly higher during heterospecific encounters than during conspecific encounters (Table II). The total number of aggressive acts per encounter was higher during heterospecific encounters but the difference was not significant (Table II).

For *P. jordani* from Kephart Prong, neither the frequencies of snap, lunge, chase and bite nor the total number of aggressive acts per encounter differed significantly between heterospecific and conspecific encounters (Table II).

For *P. glutinosus* from all three localities, neither the frequencies of individual aggressive behaviour patterns nor the total number of aggressive acts per encounter differed significantly between conspecific and heterospecific encounters (Table III). The lack of significance was not due to small sample sizes, because pooling the data from all localities did not increase the significance of the difference.

Individuals of both species from Kephart Prong were less aggressive toward both conspecifics and heterospecifics than salamanders from Courthouse Creek and Heintooga. Although salamanders from Kephart Prong were kept in captivity longer than

Table II. Mean frequencies of aggressive behaviour patterns performed by adult *P. jordani* from three localities during 45-min encounters with heterospecifics and conspecifics

Behaviour	Conspecific		Heterospecific		
	$\bar{X}$	SE	$\bar{X}$	SE	P*
Courthouse Creek (*N* = 11)					
Snap	3·18	1·46	0·45	0·28	0·031
Lunge	0·64	0·24	1·18	0·74	NS
Chase	1·64	0·58	0	0	0·008
Bite	4·82	1·38	2·27	1·34	0·039
Total	10·28	2·81	3·90	2·18	0·039
Heintooga (*N* = 15)					
Snap	0·87	0·43	4·27	2·09	0·031
Lunge	1·27	0·67	1·53	0·78	NS
Chase	0·53	0·27	0·80	0·50	NS
Bite	3·00	0·89	5·13	2·12	NS
Total	5·67	1·76	11·73	4·87	NS
Kephart Prong (*N* = 13)					
Snap	1·23	0·77	0	0	NS
Lunge	0·92	0·37	0·92	0·31	NS
Chase	0·31	0·13	0·15	0·15	NS
Bite	2·00	0·85	1·92	0·51	NS
Total	4·46	1·51	2·99	0·77	NS

* The probability that the frequencies differ beween encounter types (Wilcoxon test, α = 0·05).

Table III. Mean frequencies of aggressive behaviour patterns performed by adult *P. glutinosus* from three localities during 45-min encounters with heterospecifics and conspecifics

Behaviour	Conspecific		Heterospecific		
	$\bar{X}$	SE	$\bar{X}$	SE	P*
Courthouse Creek (*N* = 12)					
Snap	0·75	0·51	1·00	0·41	NS
Lunge	0·33	0·22	0·17	0·11	NS
Chase	0·17	0·17	0·08	0·08	NS
Bite	3·50	1·96	0·50	0·36	NS
Total	4·75	2·48	1·75	0·87	NS
Heintooga (*N* = 9)					
Snap	2·11	1·36	1·22	0·80	NS
Lunge	1·78	1·02	1·44	1·04	NS
Chase	0·44	0·29	0	0	NS
Bite	3·11	1·29	1·67	0·75	NS
Total	7·44	3·08	4·33	2·08	NS
Kephart Prong (*N* = 12)					
Snap	0·25	0·25	0·08	0·08	NS
Lunge	0·33	0·33	0·17	0·17	NS
Chase	0·25	0·25	0	0	NS
Bite	0·92	0·61	0·67	0·33	NS
Total	1·75	0·90	0·92	0·48	NS

* The probability that the frequencies differ between encounter types (Wilcoxon test, α = 0·05).

salamanders from the other localities, the length of time in captivity was not significantly correlated with the frequency of aggressive behaviour. The difference is probably due to the fact that the Kephart Prong observations were made in winter when the salamanders are normally inactive underground. It seems unlikely that the difference in the timing of the observations affected the interpretation of statistical tests comparing the response of an individual salamander to conspecifics and heterospecifics presented at 2-day intervals. However, the Kephart Prong data are not directly comparable to the data from other localities because the observations were made at a different time of year.

DISCUSSION

For *P. glutinosus*, the misidentification theory is sufficient to account for the pattern of variation in interspecific aggression. There was no evidence that *P. glutinosus* from any locality distinguishes behaviourally between heterospecific and conspecific intruders. This does not imply that the salamanders are incapable of recognizing heterospecifics. Several studies have suggested that *Plethodon* species have the ability to recognize species-specific odours (Jaeger & Gergits 1979; Dawley 1984); however, *P. glutinosus* apparently does not use this information to modify its aggressive responses to intruders. Because the relative frequency of interspecific aggression did not vary concordantly with the frequency of hybridization, it is unlikely that aggressive misidentification and reproductive misidentification have a common causal basis in *P. glutinosus*.

In a previous study, I found that the absolute frequency of interspecific aggression was significantly higher for *P. glutinosus* from Heintooga than for *P. glutinosus* from Courthouse Creek (Nishikawa 1985a). Combining the results of these two studies, it appears that *P. glutinosus* is more aggressive to *P. jordani* in localities where interspecific competition is strong than in localities where it is weak, although aggressive behaviour is not species-specific in any of the localities. Thus, in

P. glutinosus from Courthouse Creek, heterospecifics and conspecifics elicit equally low frequencies of aggression, while in *P. glutinosus* from Heintooga, heterospecifics and conspecifics elicit equally high frequencies of aggression. As pointed out by Murray (1981) and Kohda (1981), aggression toward ecological competitors resulting from misidentification may be beneficial to the aggressive individual. The interspecific aggressive behaviour of *P. glutinosus* appears to be an example of beneficial misidentification.

The observed pattern of variation in interspecific aggression in *P. jordani* cannot be explained by variation in the intensity of either intraspecific competition or intraspecific aggression. Thus, misidentification can be rejected as the process by which interspecific aggression has evolved in *P. jordani*. *P. jordani* from the locality where interspecific competition is less intense were more aggressive to conspecifics than to heterospecifics. However, *P. jordani* from both localities where interspecific competition is more intense were as aggressive to heterospecifics as they were to conspecifics. Alpha-selection is sufficient to account for this pattern of variation in interspecific aggressive behaviour among the localities, although it is not possible to falsify the hypothesis that interspecific aggression has evolved in response to some unknown variable that covaries with the intensity of interspecific competition rather than with interspecific competition itself. The result supports Hairston's (1980b, 1983b) conclusion, based on demographic data, that alpha-selection for interspecific interference has occurred in *P. jordani* from the Smoky Mountains.

The difference between species in the mode of evolution of aggressive behaviour may perhaps be related to the relative abundance of each species in the habitat. Generalized aggression may be more likely to evolve among less abundant species (e.g. *P. glutinosus*) that are confronted with a more abundant competing species. Species-specific interference may be more likely to evolve among more abundant species (e.g. *P. jordani*) in which most competitors are conspecifics, especially if heterospecifics are stronger competitors than conspecifics, as occurs in the Smoky Mountains populations of *P. jordani*.

Lastly, it is important to note that geographic variation in ecological interactions is necessary for the analysis of the selective pressures acting in the different populations. Without the observations of

P. jordani from Courthouse Creek, the absence of a significant difference between intraspecific and interspecific aggression in *P. jordani* from Heintooga and Kephart Prong would have been consistent with the misidentification theory. The variation in ecological and behavioural interactions exhibited by populations of *P. jordani* and *P. glutinosus* is exceptional among vertebrates. For most species, intraspecific and interspecific aggression have been compared under only one set of ecological conditions. In most cases, alpha-selection could not be distinguished from misidentification, and adaptation could not be distinguished from exaptation.

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