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A game model for dominance relations among group-living animals

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Abstract We present here an attempt to understand behaviors of dominant individuals and of subordinate individuals as behavior strategies in an asymmetric "hawk-dove" game. We assume that contestants have perfect information about relative fighting ability and the value of the resource. Any type of asymmetry, both relevant to and irrelevant to the fighting ability, can be considered. It is concluded that evolutionarily stable strategies (ESSs) depend on the resource value (V), the cost of injury (D), and the probability that the individual in one role will win (x). Different ESSs can exist even when values of V, D, and x are the same. The characteristics of dominance relations detected by observers may result from the ESSs that the individuals are adopting. The model explains some characteristics of dominance relations, for example, the consistent outcome of contests, the rare occurrence of escalated fights, and the discrepancy between resource holding potential (RHP) and dominance relations, from the viewpoint of individual selection.

Key words Dominance · Hawk-dove games · Resource-holding potential · Asymmetry · Evolutionarily stable strategy

Introduction

Dominance hierarchies are found among members of groups of social-living animals of a wide variety of taxonomic groups (Bernstein 1981). Dominance relations between two individuals in a group are characterized by a consistent outcome of agonistic interactions (Drews 1993). For example, in reported observations of a provisioned group of Japanese macaques (*Macaca fuscata*), one individual consistently supplanted the other in 611 out of 630 dyads, one individual inconsistently supplanted the other in 14 dyads, and the episodes ended inconclusively in 5 dyads (Takahata 1991). It is common for agonistic interactions to be less severe once dominance relations between participants are established. Direct agonistic interactions rarely occur during feeding in wild groups of Japanese macaques (Mori 1977; Furuichi 1983; Saito 1996), because the subordinate individuals appeared to avoid the dominants in wild groups during feeding (Furuichi 1983; Saito 1996).

Dominance depends on various factors among species. In many species, it is thought that dominance is determined by individual fighting ability or RHP (resource holding potential: Maynard Smith and Parker 1976). In some species, however, dominance among members depends on their matrilineal lineage (female macaques, *Macaca* spp.: Kawamura 1965; Missakian 1972; Furuichi 1983; Takahata 1991; spotted hyaenas (*Crocuta crocuta*): Frank 1986), or on the duration of tenure in the group as a result of subordination of newly joined individuals to group members (male macaques: Norikoshi and Koyama 1974; van Noordwijk and van Schaik 1985; zebras (*Equus zebra*): Rasa and Lloyd 1994; lizards (*Anolis aeneus*): Stamps 1984; juncos (*Junco hyemalis*): Cristol et al. 1990; Holberton et al. 1990; Wiley 1990). Dominance in some species is influenced by age, with older individuals generally being subordinate to younger individuals of the same sex (Hanuman langurs, *Presbytis entellus*: Borries et al. 1991; howler monkeys, *Alouatta palliata*: Jones 1980). Dominance in some birds is greatly influenced by plumage characteristics (Holberton et al. 1989). The variations suggest that dominance would not be determined simply by individual RHP.

The objective of our present analysis was to understand specific characteristics of dominance, namely (1) the consistent outcomes of contests, (2) the rare occurrence of escalated fights, and (3) variations in domi-

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nance relations among populations or species from the viewpoint of evolutionary biology.

Although several models on the evolution of dominance have been proposed (Popp and DeVore 1979; Chapais and Schulman 1980; Shively 1985; Hausfater et al. 1987; Chapais et al. 1991), few models give sufficient explanations to the above characteristics. Group- or species-advantage arguments can provide an explanation for the consistent outcomes of contests and the rare occurrence of direct fights for resources in a social group, in other words, functions to facilitate coexistence within a group and to bring harmony and stability to the group (de Waal 1986; Takahata 1991). From the viewpoint of evolutionary biology, however, the evolution of behavior that benefits a group or species rather than the individual performing it seems unlikely to occur (Maynard Smith and Price 1973), although group selection may be possible if certain conditions are fulfilled (Wilson and Sober 1994).

It has been argued that dominance hierarchies have evolved because the reproductive success of high-ranking individuals is higher than that of low-ranking ones (Shively 1985; Ellis 1995). Higher reproductive success of high-ranking individuals might cause the evolution of some traits that help the individuals to become dominant. However, important characteristics of dominance, such as the consistent outcomes of contests and the rare occurrence of escalated fights, remain unexplained. In other words, this argument does not predict how subordinate individuals will behave (cf. Rowell 1974). We must consider behaviors that results in observed dominance relations between individuals because dominance is a relationship between individuals (Bernstein 1981). Since optimal behavioral strategies vary according to the behavior of others, ESS (evolutionarily stable strategy) models (Maynard Smith 1982) that deal with the costs and benefits of behavior are indispensable.

Here we try to explain the evolution of dominance by an extension of the model of Hammerstein (1981), which examined contest situations in which two opponents differed in fighting ability as well as ownership status. The objective of the present paper is to understand actual behavior of dominant individuals and of subordinate individuals as behavior strategies in a kind of the asymmetric hawk-dove games. It will be shown that any kind of asymmetry may be used for conventional settlement of conflicts according to dominance, and that the differences in apparent dominance relations between species or populations may depend on the differences in ESSs.

Methods

Definitions and basic concepts

The definitions and basic concepts in the present model follow those of Hammerstein (1981). Roles are defined as a combination of variables, e.g., ownership status and/or relative body color. These variables are referred to as aspects of a role. A contest situation is characterized by a pair of roles (A, B). Contest situations are assumed to be asymmetric (A ≠ B). This model treats conflicts with perfect information, for which roles are unambiguously paired. The assessment of relative fighting ability and the value of the resource is assumed to be unambiguous and without cost.

Contest situations and choices

In a simple model of aggressive competition for resources and social dominance (Popp and DeVore 1979), conflict is a kind of war of attrition (Maynard Smith 1982). We use the hawk-dove model instead of the war of attrition model, because it seems simpler and more appropriate to assume that animals choose tactics of either escalation or retreat rather than choosing the timing of retreat.

In the present model, one individual plays role A and another plays role B at each contest. Roles A and B may stand for any kind of asymmetry, for example, asymmetry in age or sex. Individuals are assumed to be fully informed about the asymmetry and, for each role, they have a choice of Hawk, Dove, or Retaliator (Maynard Smith and Parker 1976; Maynard Smith 1982), defined as follows:

1. H (hawk): escalate and continue until injured or until opponent retreats
2. D (dove): display; retreat at once if opponent escalates
3. R (retaliator): start by displaying but escalate if opponent escalates

In the model of Hammerstein (1981), roles has two aspects, one of them being payoff-irrelevant (ownership status), the other payoff-relevant (relative size). Relative fighting ability between two individuals is supposed to be an increasing function of their relative size. We will consider only one asymmetry other than relative fighting ability. Roles in the present model depend on this asymmetry. This asymmetry may be irrelevant to fighting ability (e.g., relative body color) or relevant to fighting ability (e.g., relative size). Contestants are assumed to have perfect information about relative fighting ability.

Parameters of the model and payoff

The parameters of the models are defined as follows.

V = Expected utility of obtaining the resource without cost.
$-D$ = Expected cost of injury.
x = Probability that the individual in role A wins an escalated fight.
$\alpha = D/V$ (index of relative seriousness of injury)

V and D for the individual in role A are assumed to be same as those for the individual in role B. Hammerstein (1981) included a parameter T, namely, expected cost of a protracted but non-escalated fight. In our model, the cost of display is assumed to be negligible, as it is in the model of Maynard Smith and Parker (1976). The payoff matrix is shown in Table 1.

The contests end as follows:

1. *H* vs. *H*, *H* vs. *R* The individual in role A injures its opponent and obtains the resource with probability x, and is injured with probability $(1 - x)$. The individual in role B obtains the resource in the latter case.
2. *H* vs. *D* H obtains the resource, and D retreats before being injured.
3. *D* vs. *D*, *R* vs. *D*, *R* vs. *R* The resource is shared equally by the two contestants. (The resource is assumed to be divisible in the present model.)

Table 1 shows that R has a slight advantage (ε) over D, as does H over R. If $\varepsilon = 0$, we find no difference between R and D in the absence of H, or between H and R when the opponent chooses H. This selective neutrality introduces difficulties into the analysis. Therefore, it is assumed that R will sometimes discover that its opponents will never escalate and will exploit the discovery, and

Table 1 The payoff matrix of the present model (ε means a slight advantage of R over D and of H over R)

		Choice in role B		
		H	D	R
Choice in role A	H	$xV-(1-x)D \backslash (1-x)V-xD$	$V \backslash 0$	$xV-(1-x)D+\varepsilon \backslash (1-x)V-xD-\varepsilon$
	D	$0 \backslash V$	$0.5V \backslash 0.5V$	$0.5V-\varepsilon \backslash 0.5V+\varepsilon$
	R	$xV-(1-x)D-\varepsilon \backslash (1-x)V-xD+\varepsilon$	$0.5V+\varepsilon \backslash 0.5V-\varepsilon$	$0.5V \backslash 0.5V$

that H has the advantage of escalating first over R, as in Zeeman (1981) and Maynard Smith (1982).

Evolutionarily stable strategies

It is assumed that individuals have perfect information about their roles, x, and α. Under these conditions it is known (Selten 1980) that a strategy pair $p-q$ is an ESS if and only if:

$E_A(p,q) > E_A(r,q)$ for all $r \neq p$ and

$E_B(p,q) > E_B(p,r)$ for all $r \neq q$

where $E_A(p, q)$ represents the expected payoffs to A when the players A, B choose p, q respectively. It is also known (Selten 1980) that an ESS in an asymmetric contest must be a pure strategy, i.e., it does not allow for any randomized choice of actions.

Results

Nine (3×3) pure strategies need to be considered with the pairs of choices for situation (A, B). The conditions under which each strategy is an ESS can be calculated. For example, H-D "play H in role A, play D in role B" is an ESS if $(1-x)V-xD<0$, or equivalently, $1-(1+\alpha)x<0$ (see Appendix). The threshold functions $f_1(\alpha)$, $f_2(\alpha)$, $g_1(\alpha)$, and $g_2(\alpha)$ are defined as

$$f_1(\alpha) = 1/(1+\alpha)$$

$$f_2(\alpha) = \alpha/(1+\alpha)$$

$$g_1(\alpha) = 1/2(1+\alpha)$$

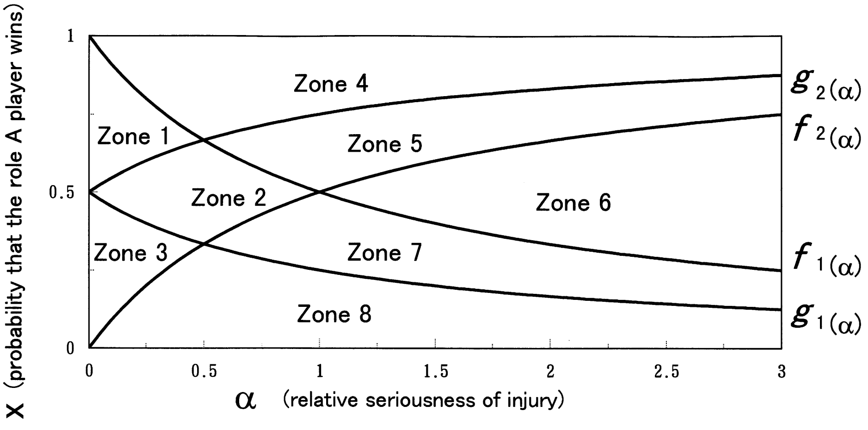
$$g_2(\alpha) = (1+2\alpha)/2(1+\alpha).$$

They give rise to eight areas in the α-x-plane, designated zones 1–8, respectively (Fig. 1). The ESSs under the each condition are shown in Fig. 1. H-D is an ESS if $f_1(\alpha) < x < 1$. D-H is an ESS if $0 < x < f_2(\alpha)$. H-H is an ESS if $f_2(\alpha) < x < f_1(\alpha)$. R-R is an ESS if $g_1(\alpha) < x < g_2(\alpha)$.

Relative RHP and ESSs

Let us assume a case where individuals recognize group members individually. We assume here that the contestants are perfectly informed about the difference in fighting ability or RHP between the contestants (x). Each individual behaves consistently towards a certain individual according to x. For simplicity, α is fixed as $\alpha 1$ in the following analysis (Fig. 2).

H-D, D-H, and R-R are ESSs in zone 6. Thus, one of the three would be adopted at a condition represented



(α, x) located in zone	Strong equilibrium pairs
1	H-H
2	H-H, R-R
3	H-H
4	H-D
5	H-D, R-R
6	H-D, R-R, D-H
7	R-R, D-H
8	D-H

Fig. 1 Threshold functions and the corresponding eight zones in the α-x plane for which different ESSs exist. The relative seriousness of injury α is defined by $\alpha = D/V$, where V is the value of winning and $-D$ is the cost of injury

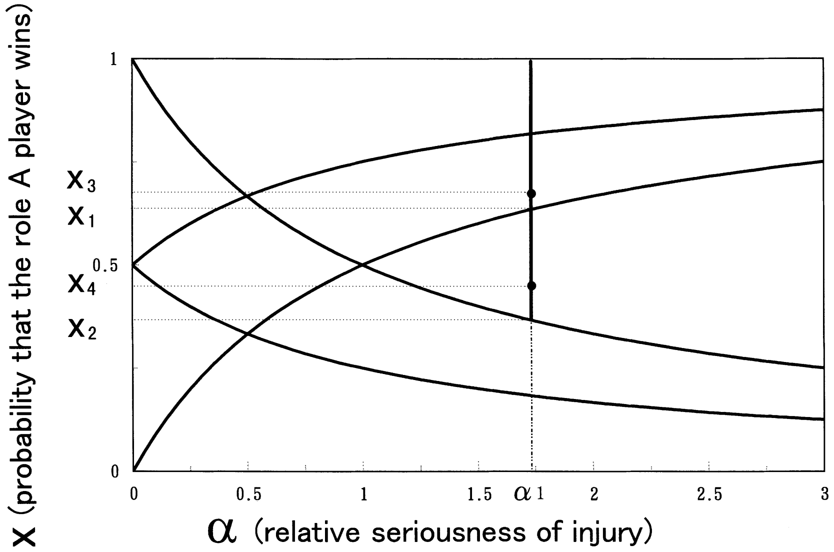


Fig. 2 Threshold functions and the corresponding eight zones in the α-x plane for which different ESSs exist. An example of a population is represented by the line $\alpha = \alpha 1$

by $x4$ by all members of each population. The strategy chosen at the population may depend on the history of each population.

The "common-sense" strategy "play H if the player is stronger than the opponent but play D if he is weaker", or "adopt H-D when $1 \geq x > 0.5$ but adopt D-H when $0.5 \geq x \geq 0$" is one possible ESS. The strategy "adopt H-D if $1 \geq x > x2$ but adopt D-H if $x2 \geq x \geq 0$" is also one possible ESS (Fig. 2). In this case, the role A player who is a little weaker than the role B player wins and obtains the resource if the difference in RHP is small ($0.5 > x > x1$). Even if a "wise" individual were to adopt the common-sense strategy, it cannot succeed in the population where all other members adopt this strategy. Consider the case where the role A player become weaker than the role B player because of aging, and the probability of winning (x) falls from $x3$ to $x4$ (Fig. 2). The role A player would still obtain the resource without an escalated fight. It does not pay the role B player to escalate the fight because the rewards are outweighed by the risk of injury although it would win more often than the role A player.

Resource value and ESSs

Let us assume that the contestants are perfectly informed about the value of the resource. Consider a simple case where individuals can distinguish between two types of resource, for example, between food and mates, or between fruits and leaves. In the former case, the evolution game is divided to two games, contests for food and contests for mates. In a population where the conditions of contests for food are represented by L and those for mates are represented by K (Fig. 3), a strategy "H-H for mates, H-D for food" is one possible ESS.

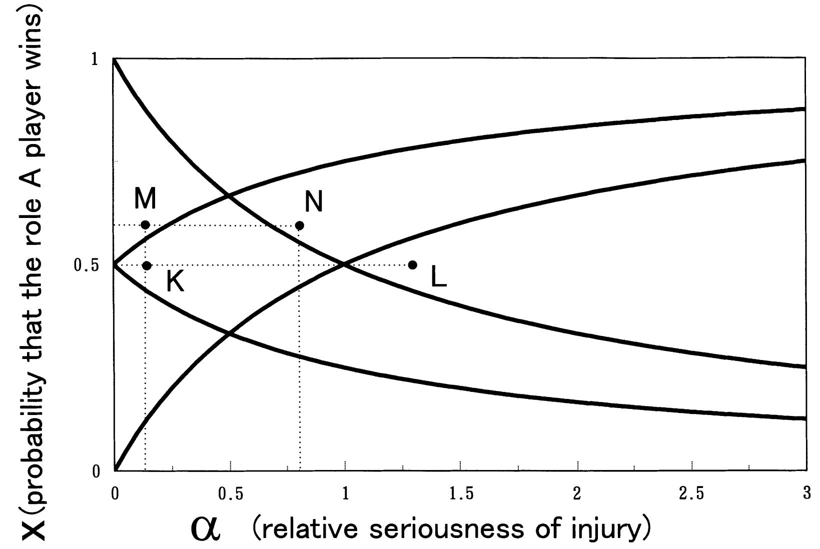


Fig. 3 Threshold functions and the corresponding eight zones in the α-x plane for which different ESSs exist. An example of a population is represented by K, L, M, and N

Thus, the outcome of contests of a certain pair of individuals would differ according to the type of the disputed resource in this population.

Difference in stability between the ESSs

Let us consider the case wherein the condition (α, x) is in zones 5 or 6. In a population where all members adopt R-R, no deviant strategies can success if the number of individuals that adopt the deviant strategy is negligible. However, if the number of individuals playing H in role A is not negligible, individuals playing D in role B are at an advantage as compared to playing R. Individuals playing H in role A might be more successful than those playing R in role A when a considerable number of individuals plays D in role B. Finally, all members of the population would adopt another ESS, H-D. By contrast, a population where all members adopt H-D is more stable than that one adopting R-R, because individuals playing D in role B are always at an advantage as compared to those playing R when there are some individuals playing H in role A. Similarly, a population where all members adopt H-D in zone 6 is more stable than one adopting D-H if $x > 0.5$.

Difference in the resource value between the contestants

Now we proceed the cases wherein the contestants differ in V and/or D (Table 2). It is easy to see that H-D is an ESS if $(1-x)V_B - xD_B < 0$, or equivalently, $x > 1/(1+\alpha_B)$. Similarly, D-H is an ESS if $x < \alpha_A/(1+\alpha_A)$, H-H is an ESS if $\alpha_A/(1+\alpha_A) < x < 1/(1+\alpha_B)$, and R-R is an ESS if $1/2(1+\alpha_B) < x < (1+2\alpha_A)/2(1+\alpha_A)$ (Appendix). Table 3 shows possible ESSs according to x, α_A, and α_B if both contestants know each other's α. For example, when (α_A, x) is in zone 5 (N) and (α_B, x) is in zone 1 (M) (Fig. 3), H-H and R-R are possible ESSs. It means that we may see escalated fights between the contestants if the resource is highly valuable for the "weaker" individual. By contrast, when (α_A, x) is in zone 1 (M) and (α_B, x) is in zone 5 (N) (Fig. 3), only H-D is a possible ESS and we do not see escalated fights.

Table 3 The possible ESSs according to α_A, α_B, and x

(α_A, x) located in zone	(α_B, x) located in zone	ESS
1	1, 2	H-H
2	3	H-H
3	3, 8	H-H
4	1	H-H
1, 4	4, 5, 6	H-D
6, 7, 8	3, 8	D-H
2	1, 2, 7	H-H, R-R
3	2, 7	H-H, R-R
5	1, 2	H-H, R-R
2	5, 6	H-D, R-R
3	6	H-D, R-R
5	4, 5, 6	H-D, R-R
6	1	D-H, R-R
6, 7	2	D-H, R-R
6, 7, 8	7	D-H, R-R
6	4, 5, 6	H-D, D-H, R-R
7, 8	6	H-D, D-H, R-R

It may be more reasonable to assume that each contestant knows only the distribution of their opponent's V and D though he knows his own V and D exactly. Contestants would choose their strategies based on their knowledge of their V and D, and on the estimated value of their opponent's V and D. If the range of estimated values is not wide, all the strategies listed in Table 3 are still ESSs though the threshold functions shift a little. When (α_A, x) is in zone 1 (M) and (α_B, x) is in zone 5 (N) (Fig. 3), only H-D is a possible ESS. However, we may see rare escalated fights due to the difference between the estimated value and the exact value of the opponent's α.

Discussion

The results of the present study show that several characteristics of dominance relations detected by observers may result from the ESSs that the individuals are adopting.

In the present model, four strategies, H-D, D-H, H-H, and R-R are possible ESSs. If all individuals in a group adopt the strategy H-D, in a certain dyad one individual consistently acquires resources while the other retreats. If all are playing D-H, one individual consistently acquires resources while the other retreats. Observers would say in each case that a "dominance relation" is found between two individuals, and they would find no differences between H-D and D-H. If all adopt H-H, individuals always fight over resources. Observers would find dominance relation in which one individual acquires resources more frequently (x) than the other does ($1-x$). They may find no dominance

Table 2 The payoff matrix when V and D are different between the contestants (ε means a slight advantage of R over D and of H over R)

		Choice in role B		
		H	D	R
Choice	H	$xV_A - (1-x)D_A \backslash (1-x)V_B - xD_B$	$V_A \backslash 0$	$xV_A - (1-x)D_A + \varepsilon \backslash (1-x)V_B - xD_B - \varepsilon$
in	D	$0 \backslash V_B$	$0.5V_A \backslash 0.5V_B$	$0.5V_A - \varepsilon \backslash 0.5V_B + \varepsilon$
role A	R	$xV_A - (1-x)D_A - \varepsilon \backslash (1-x)V_B - xD_B + \varepsilon$	$0.5V_A + \varepsilon \backslash 0.5V_B - \varepsilon$	$0.5V_A \backslash 0.5V_B$

relation if the difference in the RHP between them is small. If all adopt R-R, individuals share resources without escalation. However, if an individual escalates because of his wrong estimation of the opponent's α, the other does not allow his claim. Therefore, counter-attacks would be observable. Observers would see rare escalated fights, and find no consistent dominance relations between individuals. They may find dominance relations in which one individual acquires resources more frequently (x) than the other does ($1 - x$), although the frequency of escalated fights is very low.

It seems reasonable to assume that injury is relatively serious as compared with the resource ($\alpha > 1$) in contests in which animals compete on a daily basis. If $\alpha > 1$, the possible ESSs are H-D, D-H, R-R, and combinations of the three strategies. Thus, rare escalated fights would be observed.

When we observe a consistent dominance relation between two individuals, the dominant individual would be expected to be stronger in RHP than the subordinate. Under the conditions represented in zone 6, however, an asymmetry may cause the weaker to become the dominant. Therefore, we may find no change in the dominance relation between the two individuals after the RHP of the dominant has declined. If the dominant become much weaker than the subordinate, however, change in dominance relation occurs inevitably. In other words, discrepancy between dominance and RHP caused by an asymmetry could be found only in zone 6.

In the present model, one individual is the role A player and another the role B player at each contest. Role asymmetry may be irrelevant to the fighting ability (e.g., relative body color) or relevant to the fighting ability (e.g., relative body size). It is worth considering the possibility that the role asymmetry is determined by a rule that the members of the population all recognize. Most female macaques might recognize the kinship rule "the mother is the role A player against her daughter, the younger sister is the role A player against the older" (Kawamura 1965; Missakian 1972; Furuichi 1983; Takahata 1991). Some animals might recognize the female-dominance rule "a female is the role A player in a contest between a female and a male" (dwarf mongooses, *Helogale parvula*: Rasa 1972; spotted hyaenas: Frank 1986; lemurs: Richard 1987), and some animals might recognize the old-timer rule "the individual whose tenure in the group is longer is the role A player" (male macaques: Norikoshi and Koyama 1974; van Noordwijk and van Schaik 1985; zebras: Rasa and Lloyd 1994, lizards: Stamps 1984; juncos: Cristol et al. 1990; Holberton et al. 1990; Wiley 1990). Individuals who challenge the dominant status could not improve their fitness if all individuals were to recognize one of the above predetermined rules.

Individuals who challenge the dominance status can improve their fitness, however, if all individuals in the population recognize a rule where the role in each dyad is changeable through a repetition of contests, as van Rhijn and Vodegel (1980) showed.

Different costs of injury relative to the value of the resource (α) or the probability of winning (x) can lead to different types of dominance relation because the possible ESSs would differ. Therefore, observers may find different dominance relations in a certain pair of individuals if the disputed resources differ (Hand 1986). For example, they may find apparent dominance relations where one individual consistently wins against another in contests over mates, while they may find no clear dominance relation in contests over food. In an extreme case, the dominant-subordinate relationship between the two individuals can be reversed. Similarly, dominance relations may differ between pairs of individuals in a group due to differences in relative RHP. Observers may find apparent dominance relations between individuals which differs greatly in RHP, while they may find no clear dominance relations between individuals which are more evenly matched (*cf.* de Waal 1991).

Moreover, several different ESSs can exist even when values of α and x are the same. Thus, dominance relations can differ between populations even when the conditions (α, x) are identical. In other words, characteristics of dominance relations in a population would not be determined simply by ecological conditions. They would considerably depend on the history of the population.

It is more often likely to be the case that V and/or D differ between contestants (Grafen 1987). For example, D may be lower for old individuals because they may have a lower expected future reproductive success than young individuals. The present result suggests that if the relative value of V for the individual weaker in RHP is large, he is likely to fight against the stronger one. This agrees with the result of Bachmann and Kummer (1980).

The problem of relative stability between the ESSs treated in the present study is related to equilibrium selection in the recent economics works (Samuelson 1997). In most cases of 2×2 symmetric games with two strict Nash equilibria, the risk-dominant equilibrium (Harsanyi and Selten 1988) is selected (Harsanyi and Selten 1988; Kandori et al. 1993; Samuelson 1997). The risk-dominant equilibrium is characterized by having the larger basin of attraction under either the best-reply or the replicator dynamics in such games (Samuelson 1997). Although the game in the present model is asymmetric, H-D has a larger basin of attraction than R-R.

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Appendix

We show the case in which V and D differ between contestants. The pay-off matrix is shown in the Table 2. If V and D are the same for both contestants, we can read $\alpha_A = \alpha_B = \alpha$.

H-D "play H in role A, play D in role B" is an ESS if the following four inequalities are satisfied:

$$E_A(\mathrm{H,D}) > E_A(\mathrm{D,D}),\ E_A(\mathrm{H,D}) > E_A(\mathrm{R,D})\ ,$$
$$E_B(\mathrm{H,D}) > E_B(\mathrm{H,H}),\ E_B(\mathrm{H,D}) > E_B(\mathrm{H,R})\ .$$

Hence

$$V_A > 0.5V_A\ ,$$
$$V_A > 0.5V_A + \varepsilon\ ,$$
$$0 > (1-x)V_B - xD_B\ ,$$

and

$$0 > (1-x)V_B - xD_B - \varepsilon\ .$$

Putting $D_B/V_B = \alpha_B$, we obtain

$$x > 1/(1+\alpha_B)\ .$$

D-H is an ESS if the following four inequalities are satisfied:

$$E_A(\mathrm{D,H}) > E_A(\mathrm{H,H}),\ E_A(\mathrm{D,H}) > E_A(\mathrm{R,H}),$$
$$E_B(\mathrm{D,H}) > E_B(\mathrm{D,D}),\ E_B(\mathrm{D,H}) > E_B(\mathrm{D,R})\ .$$

Hence

$$0 > xV_A - (1-x)D_A\ ,$$
$$0 > xV_A - (1-x)D_A - \varepsilon\ ,$$
$$V_B > 0.5V_B\ ,$$

and

$$V_B > 0.5V_B + \varepsilon\ .$$

Putting $D_A/V_A = \alpha_A$, we obtain

$$x < \alpha_A/(1+\alpha_A)\ .$$

H-H is an ESS if the following four inequalities are satisfied:

$$E_A(\mathrm{H,H}) > E_A(\mathrm{D,H}),\ E_A(\mathrm{H,H}) > E_A(\mathrm{R,H})\ ,$$
$$E_B(\mathrm{H,H}) > E_B(\mathrm{H,D}),\ E_B(\mathrm{H,H}) > E_B(\mathrm{H,R})\ .$$

Hence

$$xV_A - (1-x)D_A > 0\ ,$$
$$xV_A - (1-x)D_A > xV_A - (1-x)D_A - \varepsilon\ ,$$
$$(1-x)V_B - xD_B > 0\ ,$$

and

$$(1-x)V_B - xD_B > (1-x)V_B - xD_B - \varepsilon\ .$$

Putting $D_A/V_A = \alpha_A$ and $D_B/V_B = \alpha_B$, we obtain

$$\alpha_A/(1+\alpha_A) < \mathrm{x} < 1/(1+\alpha_B)\ .$$

R-R is an ESS if the following four inequalities are satisfied:

$$E_A(\mathrm{R,R}) > E_A(\mathrm{H,R}),\ E_A(\mathrm{R,R}) > E_A(\mathrm{D,R})\ ,$$
$$E_B(\mathrm{R,R}) > E_B(\mathrm{R,H}),\ E_B(\mathrm{R,R}) > E_B(\mathrm{R,D})\ .$$

Hence

$$0.5V_A > xV_A - (1-x)D_A + \varepsilon,$$
$$0.5V_A > 0.5V_A - \varepsilon\ ,$$
$$0.5V_B > (1-x)V - xD_B + \varepsilon\ ,$$

and

$$0.5V_B > 0.5V_B - \varepsilon\ .$$

Putting $D_A/V_A = \alpha_A$ and $D_B/V_B = \alpha_B$, we obtain

$$1/2(1+\alpha_B) < x < (1+2\alpha_A)/2(1+\alpha_A)\ .$$

For D-D, H-R, D-R, R-H, and R-D, the four inequalities are not satisfied simultaneously.

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