Breeding Games and Dimorphism in Male Salmon

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Abstract

In certain species of salmon, male phenotypes occur in two distinct morphs: the large "hooknose" (H) or the small "jack" (J). Hooknoses fight each other for access to females, while jacks occupy refuges near spawning beds to sneak fertilizations.into the breeding bed of a pair. Jacks also fight each other over opportunities for sneaking without immediate gains. To explore whether the jack behavioural strategy is equally adaptive to that of the hooknose, we built a game-theoretic model similar to the classic hawk-dove game, with and without conditions of density dependence. Our model We demonstrates the fitness of the jack strategy increases with the frequency of the hooknose strategy, because jacks can steal the benefits otherwise accrued by hooknoses. The In this game, coexistence of strategies strategy coexistence is much more easily achieved in this game than in the hawk-dove game. When negative density effects on benefits are introduced to the model, coexistence conditions are further relaxed. Hence, the jack and hooknose strategies can be viewed as equally adaptive, resulting in a stable mixed ESS. When the hooknose-jack game is considered an evolutionary game, frequencies of the two morphs either yield a balanced polymorphism or the fitness function of the hooknose proportion increases. In the latter case, jack becomes a dominant strategy.

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Keywords: morph, jack, hooknose, coexistence, game-theoretic model, fitness, alternative

mating strategy, evolutionarily stable strategy, conditional strategy, hawk-dove game

59 In many animal species, competition among males for mating privileges is prevalent

60 (Krebs & Davies 1987). Such rivalries may favour selection for male dimorphism, alternative

61 mating strategies, or both. The hawk-dove game was developed as a means of understanding the

62 theoretical basis of animal conflict (Maynard Smith & Price 1973), and the evolutionary game

63 of animal fighting in particular (Bulmer 1994). However, it has only rarely been applied to the

64 evolutionary ecology of mating systems.

65

66 In a number of salmonid fishes, mMales in some salmonids are distinctly dimorphic in

67 body size, external morphology and life history (Gross 1984, 1985). L A large breeding males,

68 called "hooknoses" (H), undergo full development, is a fullyhaving spent matured male

69 spending two toor three years at sea before returning to theirits natal rivers to spawn with

70 females. Hooknoses develop display courtship colouration and a hooked nose with sharp teeth

71 for fighting. ByIn contrast, a small males, called "jacks" (J), undergo limited development and

72 resembles an immature fish. As juveniles, precocious males become jacks and return to

73 spawning beds at least one year before hooknoses (Gross 1991). Hooknose males battle other

74 hooknoses for access to females. However, Jjacks, however, seek refuges sneak near the

75 breeding grounds of a paired fish, from which they sneak to release sperm and swim through the

76 beds releasing sperm immediately following female spawning.

Hooknose and jack are considered alternative strategies (Gross 1982; Thornhill & Alcock 1983) or conditional mating strategies (Gross 1996). Gross (1984) considered such alternative mating strategies as evolutionarily stable strategies (ESSs) (Maynard Smith 1982), provided the payoffs of both H and J are equal. If the payoff of J is smaller than that of H, the jack strategy is the less fit conditional mating tactic. Gross also found that the lifetime fitnesses of H and J in coho salmon (*Oncorhynchus kisutch*) are about equal at their switchpoint, indicating the mixed strategy of both H and J is an evolutionarily stable strategy (ESS) (Maynard Smith 1982; Gross 1985). Thus Gross (1984, 1985) suggested that the dimorphism in male salmon might have evolved through an evolutionary game. However, as far as we know, its explicit its payoff matricesx, withas well as and the ESS conditions for coexistence of alternative strategies, have not been examined explicitly in the context of a hawk-dove game.

Competition among male animals for mating privileges is very common (Krebs & Davies 1987). Such competition may favor selection for male dimorphism, alternative mating strategies, or both. The hawk-dove game was developed as a means of understanding the theoretical basis

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95 of animal conflict (Maynard Smith & Price 1973), and the evolutionary game of animal fighting

96 in particular (Bulmer 1994). However, it has rarely been applied to the evolutionary ecology of

97 mating systems.

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100 Recently, A recent version of the hawk-dove game has been developed to further our

101 understanding of dimorphic male strategies in male orangutans our group showed that male

102 dimorphism in the orangutan could be explained by a version of the hawk-dove game (Tainaka

103 et al. 2007). However, life--history considerations for evolutionary games differ substantially

104 between the orangutan and salmon. In the orangutan, subordinate adult males can switch

105 conditionally to a dominant phenotype, whereasile a dominant morphs –cannot switch back to

106 thea subordinate phenotype. In salmon, the choice between developing into a hooknose or a jack

107 reflects early developmental differences in individual life history and is absolutely irreversible

108 (Gross 1985, 1991). Gross further suggested juvenile body size, a strong predictor of mating

109 strategy, is a function of population density Gross 1991). Published estimates of additive genetic

110 variance indicate heritability for the choice of strategy, at least as a contributing factor

111 highlighting the potential genetic basis of alternative phenotypes (Silverstein & Hershberger

112 1992; Gross 1996; Gross & Repka & Gross 19958; Gross & Repka 1998a, 1998b). Any

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113   underlying genetic mechanisms regulating salmon dimorphism may be similar to genetic

114   polymorphisms in the fruit fly (Fitzpatrick et al. 2007) or scale-eating cichlid fish (Hori 1993;

115   Takahashi & Hori 1994).

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117

118   Here we show that male dimorphism in salmon can be explained by a breeding game

119   similar to the hawk-dove game. We build a payoff matrix for two mating strategies of male

120   salmon: Hooknose and Jack. We analyze the ESS conditions according to the benefits and costs

121   of win and lose outcomeswinning and losing, including an explicit examination of the effects of

122   population density. We also discuss the utility and generality of hawk-dove-like games in male

123   dimorphisms and alternative mating strategies.

124

125

126   **HOOKNOSE-JACK MODEL**

127

128   Our game model resembles that of the hawk-dove game (Maynard Smith & Price 1973).

129   For our purposes, By "hawk vs. dove" is equivalent towe mean "dominant vs. subordinate" or,

130   more generally, "honest contestanty competitor vs. cheater." The pay-off matrix for a male

131 salmon is given in Table 1. A hooknose (H) fights with others. The winning hooknose~~er~~ gets the

132 benefit *V* (mating value), while the loser suffers the fighting cost *C*. Hence t~~T~~he average payoff

133 for a hooknose is (*V-C*)/2. A hooknose can defeat a jack (J) easily, but a jack can sneak in and

134 spawn surreptitiously. By sneaking fertilizations from hooknoses, a jack obtains ~~So, a jack robs~~

135 the benefit *G* (on the average) ~~by sneaking~~, while the~~a~~ hooknose loses *G*, ~~resulting in~~yielding

136 the payoff *V-G*. ~~Unlike the well-known "dove," which does not fight, a jack battles other jacks~~

137 ~~over positions advantageous for sneaking. The winning jack gains fitness value *J*. The losing~~

138 ~~jack suffers cost *J-L*; therefore, the~~ the average jack ~~fighting cost~~ of fighting between jacks is

139 ~~*J-L*~~/2, since one ~~jack~~ will lose~~s~~. ~~Because of the great disparity in body size between hooknose~~

140 ~~and jack, we assume that *V>G*>0 and *C>J>L*>0. In reality, both benefits and costs of fighting~~

141 ~~between hooknoses should be very large and those of jacks should be relatively small, so that~~

142 ~~*V>>G*, and *C>>JL*.~~

143 Unlike the well-known "dove," which does not fight, a jack battles other jacks over positions

144 advantageous for sneaking. The losing jack suffers cost *L*. On the other hand, the winning jack

145 gains control of the refuge from which he can sneak, ~~the sneaking position~~but ~~only~~ without

146 immediate benefits.~~.~~ For now, we simply assume that the winning jack ~~has no~~ gains nothing.

147 Therefore, the average cost to jacks of fighting ~~jack fighting cost~~ is *L*/2, since one will lose.

148 Because of the great disparity in body size between hooknose and jack, we assume that *V>G*>0

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and $C>L>0$. In reality, both benefits and costs of fighting between hooknoses should be very large and those of jacks should be relatively small, so that $V>>G$, and $C>>L$.

The payoffs in Table 1 differ from those of the classic~~usual~~ hawk-dove game in all values except that of H vs. H. Without considering the population size of male salmon, the ~~Now we assume a constant population size of male salmon and find the~~ fitness values of both hooknose and jack can be evaluated by the traditional ESS analysis (that implicitly assumes an infinite population size) (see Riley 1979; Fogel et al. 1998; Taylor et al. 2004). Let p be the proportion of hooknose in the population. Then the fitness of a hooknose $W_H(p)$ is represented by Equation (1) (Table 2).

$$W_H(p) = p\frac{V-C}{2} + (1-p)(V-G) = (V-G) - p\left(\frac{V+C}{2} - G\right). \qquad (1)$$

On the other hand, the fitness of a jack $W_J(p)$ is represented by Equation (2) (Table 2).

$$W_J(p) = pG + (1-p)\frac{-L}{2} = \left(\frac{L}{2}\right) + p\left(G + \frac{L}{2}\right). \qquad (2)$$

167

168 WE NEED TO SUBSTITUTE J-L/2 FOR -L/2 HERE AND ELSEWHERE

169 Note that $W_J(p)$ is an increasing function of the hooknose proportion p. This is because

170 jacks who steal the benefits fromof H fight other jacks. We now examine $W_H(p)$ and $W_J(p)$ for

171 $0 \leq p \leq 1$ (Fig. 1). At $p=0$, $W_H=V-G > W_J = J-L/2$. At $p=1$, Thus, the condition for coexistence, with

172 is $W_H < W_J$ at $p=1$. This condition, is Equation (3) (Table 2).

173

174 $$G > \frac{V-C}{2}. \qquad (3)$$

175

176 When fighting between hooknoses is severe, that is, $V<C$, condition (3) is always true (Fig.

177 1a). This is the same result as coexistence of evolutionary strategies in the hawk-dove game. On

178 the other hand, when fighting between hooknoses is not so severe (i.e., is mild), that is, $V>C$,

179 condition (3) is not always true (Fig. 1b). When $V>C$, the condition (3) incurringgiving cost C

180 can be expressed as Equation (4) (Table 2).

181

182 $$V > C > V - 2G. \qquad (4)$$

183

184 Therefore, the fighting cost C of H should be close to V, the benefit of jack G should be rather

small, or both. From condition (4), if $2G>V$, condition (3) automatically holds (see Fig. 1b).

In either case, the ESS mixed frequency~~ratio~~ p^* is solved by $W_H(p) = W_J(p)$, and we get Equation (5) (Table 2).

$$p^* = \frac{2(V-G)+L}{V+C+L} \qquad (5)$$

However, the ESS becomes a~~the~~ pure hooknose strategy (i.e., $p^*=1$), if Equation (6) (Table 2) holds.

$$G < \frac{V-C}{2} \qquad (6)$$

This equation implies that, if the benefit to jacks of sneaking (G) is less than half the benefit when H wins, then the ESS is a pure hooknose strategy.

When $V>C$, the slope of W_H (=G-($V+C$)/2) can be positive, if Equation (7) (Table 2) holds.

203 ThisIt

$$2G - C > V \qquad (7)$$

207 This means means that the fitness W_H of a hooknose is an decreasing increasing (NOT DECREASING?)function of the ratio frequency of p. Even under this condition, the ESS frequencyratio $p*$ becomes the mixed strategy given by equation (5), since condition (4) holds, i.e., $2G+C>2G-C>V$. Here, if $p<p*$, jack is a poor strategy, yielding lower fitness than hooknose. When p is an increasing function, the fitness of hooknose deincreases (NOT DECREASES?) until p reaches $p*$. When $p>p*$, since jack enjoys a higher fitness payoffvalue, the frequency of jacks increases, reducing p until it reaches $p*$. Here, ironicallyremarkably, a pure hooknose strategy has higher fitness than that of the mixed ESS strategy $p*$. Similarly, when the slope of W_H ($=G-(V+C)/2$) is zero, the fitness of a hooknose is constant and that of a jack determines the mixed ESS strategy, as long as equation (3) holds.

THE EFFECT OF DENSITY

Competition among individuals for limited mates or breeding sites may increase as a function of population size, N (Tainaka et al. 2006), thus lowering the *per capita* likelihood of mating. Consequently, the benefits of breeding, V and G, may be inversely related to N. We now examine the effect of density on our hooknose-jack model.

Assume that mating values, V and G, depend on population size N, according to a simple function of density, $B / (B+N)$, where B is a constant. By multiplication we obtain the effective values of breeding, V_N, and G_N, now reduced as a function of density: Equations (8a) and (8b) (Table 2).

$$V_N = V \frac{B}{B+N}$$
$$G_N = G \frac{B}{B+N}$$
(8a, 8b)

The average net payoff for hooknose and jack individuals is given by Equations (9) and (10) respectively (Table 2), which

238 $$W_H(p,N) = p\frac{V_N - C}{2} + (1-p)(V_N - G_N) \tag{9}$$

240 $$W_J(p,N) = pG_N + (1-p)\frac{-L}{2}. \tag{10}$$

242 ~~Equations (9) and (10)~~ are similar to equations (1) and (2). Given any constant value of N,

243 they are negatively (or positively) sloped, straight lines in W-p space, as in the slope of

244 equations (1) and (2).

247 To find p^*, we examine $W_H(p, N)$ and $W_J(p, N)$ at $p=0$ and $p=1$. When $p=0$, $W_H(0, N) =$

248 V_N-$G_N = V$-G $(B/(B+G)) > W_J(0, N) = $ ~~J~~-$L/2$. Therefore, the condition for coexistence of jack

249 and hooknose is $W_H(1, N) < W_J(1, N)$ at $p=1$, as in the density-independent hooknose-jack

250 model. ~~The condition for coexistence is then~~Hence we get ~~e~~Equation (11) (Table 2). Equation

251 (12)

253 $$G_N > \frac{V_N - C}{2}$$

254 (11)

It follows from condition (11) that Equation (12) (Table 2).

$$V > C > (V - 2G)\frac{B}{B + N}$$

(12)

This condition is identical to equation (4), except for the difference term in the right-hand side of the inequality.

Since $B / (B+N)$ becomes smaller when N increases, this condition is satisfied easily when N is large. Therefore, a jack can readily coexist with a hooknose, provided the population size N is large. Even if $C < (V-2G)$, equation (11) may hold if $N>>0$, as shown inthat is, eEquation (13) (Table 2). This means that the ESS $p*$ is a pure hooknose strategy (H) when N is small, but may shift to the mixed strategy (H and J), when the population size N increases. Assuming the number of breeding sites is limited, the ESS strategy becomes density-dependent.

$$V - 2G > C > (V - 2G)\frac{B}{B + N}$$

(13)

274

275 ~~This means that the ESS $p*$ is a pure hooknose strategy (H) when N is small, but may shift~~

276 ~~to the mixed strategy (H and J), when the population size N increases.~~ Assuming the number of

277 breeding sites is limited, ~~In this case,~~ the ESS strategy becomes density-dependent.

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280 **DISCUSSION**

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282 Our model differs substantially from prior examples of ~~The current example is very~~

283 ~~different from those in~~ the hawk-dove game (Maynard Smith & Price 1973; Maynard Smith

284 1982; Axelrod & Hamilton 1981) and the orangutan game (Tainaka et al. 2007) (see Fig. 2). In

285 these games, t~~T~~he slope of subordinates/doves is negative as well as those of hawks/dominants

286 ~~in these games~~ (Fig. 2c). By contrast~~However~~, in the hooknose-jack game presented here, the

287 fitness of jack, W_J, is an increasing function of p, while that of hooknose, W_H, is a decreasing

288 function of p (Fig. 2a). Thus~~erefore~~, th~~is~~ constitute~~s~~ ~~salmon game in this condition is~~ a true

289 balancing game with negative frequency dependence (Figs. 1 and 2a), similar to the genetic

290 polymorphism maintained by negatively frequency-dependent selection (e.g., Hori 1993;

291 Takahashi & Hori 1994; Fitzpatrick et al. 2007). Furthermore, the fitness of hooknose, W_H, can

292 be an increasing function, too, if equation (7) holds (Fig. 2b). ~~In this case, we can~~Now, if we

293 replot Fig. 2b ~~against~~ with the jack proportion defined as q (=1-p)~~.~~, ~~Then,~~ the graph becomes

294 identical to Fig. 2c. ~~However,~~Here, the payoff of jacks and hooknoses is reversed, in spite of the

295 fact that jacks are poor competitors with hooknoses in direct contests over mating privileges.

296 ~~meaning of jack is reversed to dominant or hawk, even though jack is a sneaker that is a weaker~~

297 ~~competitor for breeding.~~

298

299 In our model, we assumed that the winning jack gains no fitness. However, the winning

300 jack may locate a better sneaking position for fertilization. Therefore, we may assume that the

301 winning jack gains the slight fitness value S, where S is ~~extremelyfar~~vastly smaller than G, that

302 is,V>G>>S>0. Because the losing jack suffers a fighting cost $-L$, the average cost of fighting

303 between jacks is (S-L)/2. Because S is very close to zero (though positive), we can ~~naturally~~

304 assume that C>>S. Therefore, (S-L) is still negative and we can ~~put~~define (S-L) = - L* Hence,

305 substituting L* for L changes none of the above ~~all~~ formulations and arguments ~~do not change,~~

306 ~~if we replace L into L*:.~~ Thus the generality of the current results holds even if the~~a~~ winner of a

307 contest between ~~ing~~sneakers ~~among a sneaker fight~~ gains a ~~minimal~~ benefit, because the

308 benefit~~it~~ is minimal.

309

310   The salmon mating system examined here ~~involves~~ assumes a large tradeoff between the

311   jack and hooknose male mating strategies. Hooknose is the dominant strategy in terms of sperm

312   quantity, body size and controlling access to females. However, the jack life history strategy,

313   being one year shorter, ~~results in~~ benefits from lower mortality rates from natural enemies in the

314   marine habitat (Gross 1991); this assures the frequency-dependent nature of fitness tradeoffs

315   between mating success and survival (Figs. 1 and 2). With such tradeoffs, the fitness equalities

316   of hooknose and jack are easily attained (Gross 1984). This may be why the hooknose-jack

317   game yields a balanced polymorphism similar to those examined in other systems such as

318   scale-eating cichlid fish (Hori 1993; Takahashi & Hori 1994) and single-locus behavioural

319   polymorphisms generally ~~is similar to those of balanced polymorphisms~~ (~~Hori 1993; Takahashi~~

320   ~~& Hori 1994;~~ Fitzpatrick et al. 2007).

321

322

323   ~~P~~The previous findings ~~seem to~~ suggest that sneakers and hooknoses coexist stably ~~are~~

324   ~~relatively stable~~ even in ~~a~~ very small populations (Gross 1984, 1985, 1991, 1996). However, the

325   traditional ESS analysis assumes an infinite population size and the evolutionary outcomes of a

326   finite population size are often unstable, ~~and/or~~ different from the ESS equilibrium, or both

327   (Riley 1979; Fogel et al. 1998; Taylor et al. 2004). In the orangutan mating system, large

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328 population sizes tend to increase the proportion of subordinate mating strategies (Tainaka et al.

329 2007). We expect that the sneaker frequency is unstable and high when population sizes are

330 small. However, our current results suggest that the frequency of jack is 0 or low at a small

331 population size and increases as the population size increases (Fig. 2). This is the reverse of

332 theoretical findings for opposite to the results of finite population sizes (Riley 1979; Fogel et al.

333 1998; Taylor et al. 2004). Furthermore, theoretical studies shows that conditional strategies like

334 sneaking are stable even if the strategies have a genetic basis (Repka and Gross 1995; Gross

335 and Repka 1998a, 1998b). The effects of population sizes may be tested empirically by

336 surveying the frequency and stability of the jack strategy in a rivers of different sizes and over

337 several years.

338

339 Previousior theoretical findings suggested that sneakers could evolve only in very small

340 populations, because sneaking is a conditional mating tactic due to arising as a result of

341 developmental disadvantages

342 , (Fogel et al. 1998; Taylor et al. 2004). I DON'T UNDERSTAND WHY SMALL

343 POPULATIONS ARE NECESSARY FOR THIS? THE TITLE OF FOGEL ET AL.'S PAPER

344 SEEMS TO SUGGEST THAT ESS'S IN SMALL POPULATIONS ARE UNSTABLE. In the

345 orangutan mating system, Recently, it was shown that high population densities tend to increase

20

346   the proportion of subordinate mating strategiess in the orangutan model (Tainaka et al. 2007).

347   Our modified model provides a further example in the literature with density effects is an

348   additional example exploring the evolution and maintenance of sneaker strategies, wherein the

349   density of resources such as mating opportunities and breeding sites varies. , density is varied.

350   e.g., mating opportunities and breeding sites. Our results suggest that We have refined the model

351   with our treatment of ddensity dependence factors, thus further promoteing the coexistence of

352   jack and hooknose strategies (equations (12) and (13)). WhenIf resources such as females and

353   breeding grounds are limited, competition for these limited resources intensifies between

354   dominants; consequently, subordinate strategies should become more adaptive, provided

355   sufficient refuges exist. since the dominants have to fight over these limited resources. For

356   example, suppose that there are only 10 breeding grounds or 10 females in a suitable spawning

357   area. If 100 hooknoses return to spawn, 90% of them (90 fish) should fail reproduction

358   completely. Furthermore, the winning 10 hooknoses may suffer severe fighting-related injuries.

359   Under such conditions, jack becomes a far superior strategy. This effect of population density is

360   similar toresembles that of the orangutan modelease, since subordinate strategies (jacks) become

361   advantageous as the population size increases (Tainaka et al. 2007). Likewise, in the colonial

362   acarid mite, *Catoglyphus berlesei*, fitness payoffs for alternative male mating strategies depend

363   on colony size: dominants (fighters) do better in small colonies; subordinates (non-fighters), in

364   large colonies (Radwan 1993).

365

366

367   The constant proportion of jacks observed in broods (Koseki & Fleming 2006) strongly

368   suggests that jack and hooknose constitute an ESS mixed strategy. During development,

369   status-dependent selection in salmon yields a conditional strategy under which precocious males

370   become jacks, and those delaying maturity become hooknoses. In fact, the sneaker life-history

371   strategy is chosen by the fastest-growing juveniles (those with the highest status) (Gross 1996),

372   although the precise mechanisms triggering developmental switches remain to be elucidated. At

373   least one author has argued the alternative tactics "fighter" and "sneaker" be regarded instead as

374   "coercer" and "cooperator," owing toFurther, there is evidence females actually prefer the more

375   cooperative jacks over aggressive hooknoses during spawning (Watters 2005). These facts

376   hardly suggest that jack is an inferior life history strategy. On the contrary, the widespread

377   occurrence of the jack strategy supports the hypothesis that jack is an integral part of a mixed

378   ESS strategy in salmonid fishes (Gross 1984, 1985).

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381   Given that sSneaker or subordinate strategies are at least partially genetically mediated,

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382 male conditional strategies may be highly adaptive for females, in terms of spreading risk

383 spreading (Yoshimura & Clark 1991; Yoshimura & Jansen 1996). If all eggs of a female are

384 inseminated by one dominant male whose sperm are genetically deficient, she ends up with no

385 reproductive success. DNA finger-printing evidence suggests that female extra-pair matings are

386 extremely common in many animal mating systems appearing otherwise monogamous (Burke

387 & Bruford 1987; Westneat 1990; Barash & Lipton 2001). Thus females may tacitly solicit

388 mating opportunities fromor sneaker or subordinate males (Watters 2005), further promoting the

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389 evolution of a mixed ESS strategy.

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391

392   Alternative mating tactics are known in many animal species (Gross 1982; Thornhill &

393 Alcock 1983; Kodric-Brown 1986). Subordinates or sneakers have been considered the less

394 adaptive strategy, because their payoffs mean fitness values appearre lower than those of

395 dominant males. However, the orangutan model (Tainaka et al. 2007) and the current model

396 presented here suggest that the subordinates or sneakers can beare as fit as dominant males,

397 resulting in a mixed ESS strategy. In many cases of breeding gamesmating systems, dimorphism

398 in males may be favored under conditions ofwhen alternative life historyontogenetic trajectories

399 involve life history trade-offs and varying population densities. In those casesUnder these

400 conditions, both morphs gain fitness. Such evolutionary games may thus be widely prevalent

401 not only in the matingbreeding games of dimorphic males, but in breeding systems generally.

402 For example, in female goldeneye ducks, population densities can play a critical role in

403 maintaining intraspecific brood parasitism as an alternative nesting strategy (Eadie & Fryxell

404 1992). Lastly, we are only beginning to understand the magnitude of anthropogenic changes to

405 the environment on life history evolution, and their effects on the stability of balanced

406 polymorphisms in commercially important taxa such as salmonids.

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482

483   Table 1. Payoff matrix of Hooknose-Jack game in salmon males (V: The benefit of winning a

484   female; C: the fighting cost of a loser; G: the benefit of sneaking; and L: the fighting cost of a

485   losing jack). We assume that $V>G>0$ and $C>L>0$.

486

487   Opponent

Player	Hooknose	Jack
Hooknose	(V-C)/2	V-G
Jack	G	-L/2

491

Table 2. Equations for Hooknose-Jack games in male salmon males

$$W_H(p) = p\frac{V-C}{2} + (1-p)(V-G) = (V-G) - p\left(\frac{V+C}{2} - G\right) \tag{1}$$

$$W_J(p) = pG + (1-p)\frac{-L}{2} = \left(-\frac{L}{2}\right) + p\left(G + \frac{L}{2}\right) \tag{2}$$

$$G > \frac{V-C}{2} \tag{3}$$

$$V > C > V - 2G \tag{4}$$

$$p^* = \frac{2(V-G)+L}{V+C+L} \tag{5}$$

$$G < \frac{V-C}{2} \tag{6}$$

$$2G - C > V \tag{7}$$

$$V_N = V\frac{B}{B+N}$$

$$G_N = G\frac{B}{B+N} \tag{8a}, \tag{8b}$$

$$W_H(p,N) = p\frac{V_N-C}{2} + (1-p)(V_N - G_N) \tag{9}$$

$$W_J(p,N) = pG_N + (1-p)\frac{-L}{2} \tag{10}$$

$$G_N > \frac{V_N-C}{2} \tag{11}$$

$$V > C > (V-2G)\frac{B}{B+N} \tag{12}$$

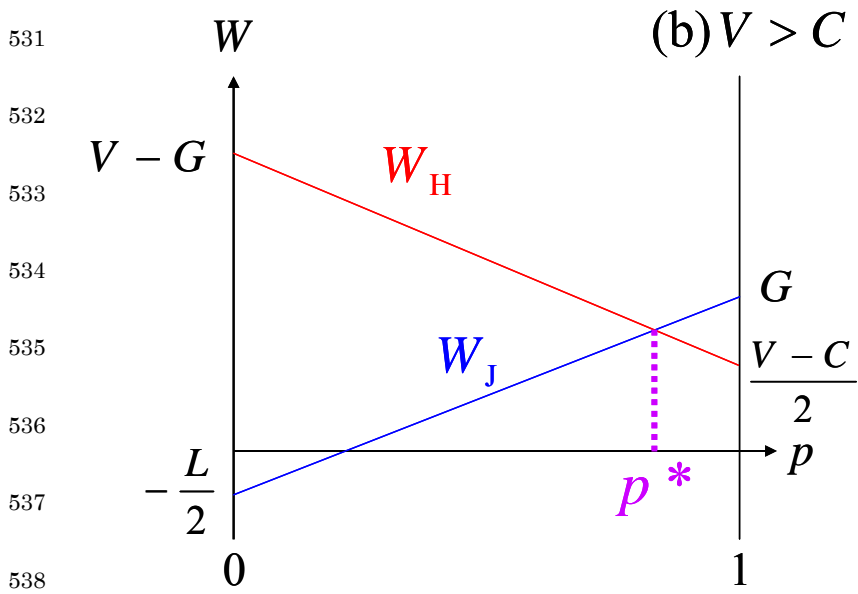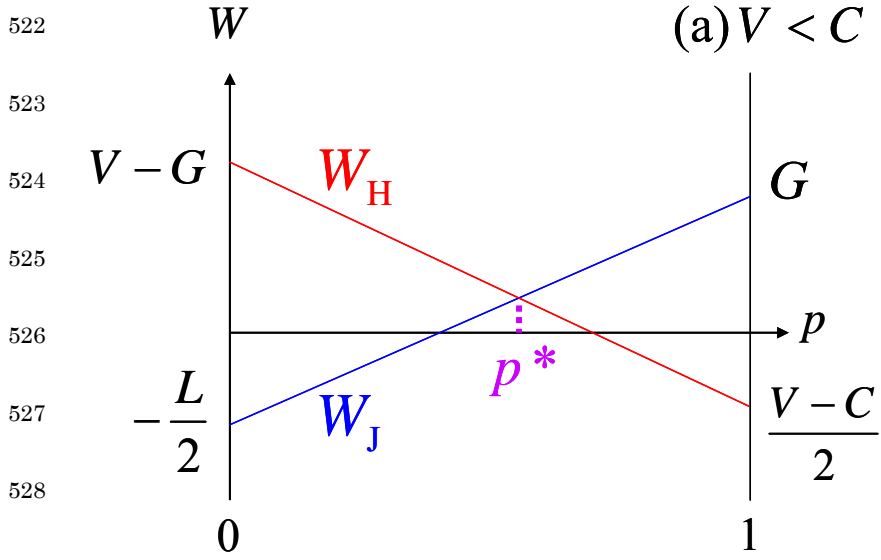$$V - 2G > C > (V-2G)\frac{B}{B+N} \tag{13}$$

30

509 **Figure legends**

510 Fig. 1. The average net payoffs (*W*) of hooknose and jack in the model. The values of $W_H(p)$ and

511 $W_J(p)$ are plotted~~depicted~~ against the frequency~~ratio~~ p of hooknose. In (a), fF~~ighting~~ between

書式変更：フォントの色 ： 赤

512 hooknose is severe, that is, $V<C$;~~,~~ and in (b) it is mild, viz.,~~that is~~ $V>C$. The intersections

513 determine a stable, mixed strategy ESS. *p** is the mixed ESS strategy.

514

515 Fig. 2. The slopes of the schematic payoffs (*W*) in the breeding games between dominants and

516 subordinates along the proportion of dominants (*p*), where *p** is the mixed ESS strategy. (a) ~~the~~

517 hooknose and jack model with negative frequency dependence, (b) ~~the~~ hooknose and jack model

518 with dual increasing payoff functions and (c) ~~the~~ hawk-dove like games with dual decreasing

519 payoff functions. W_H, W_J, W_D and W_S represent the fitness values of hooknose, jack, dominant
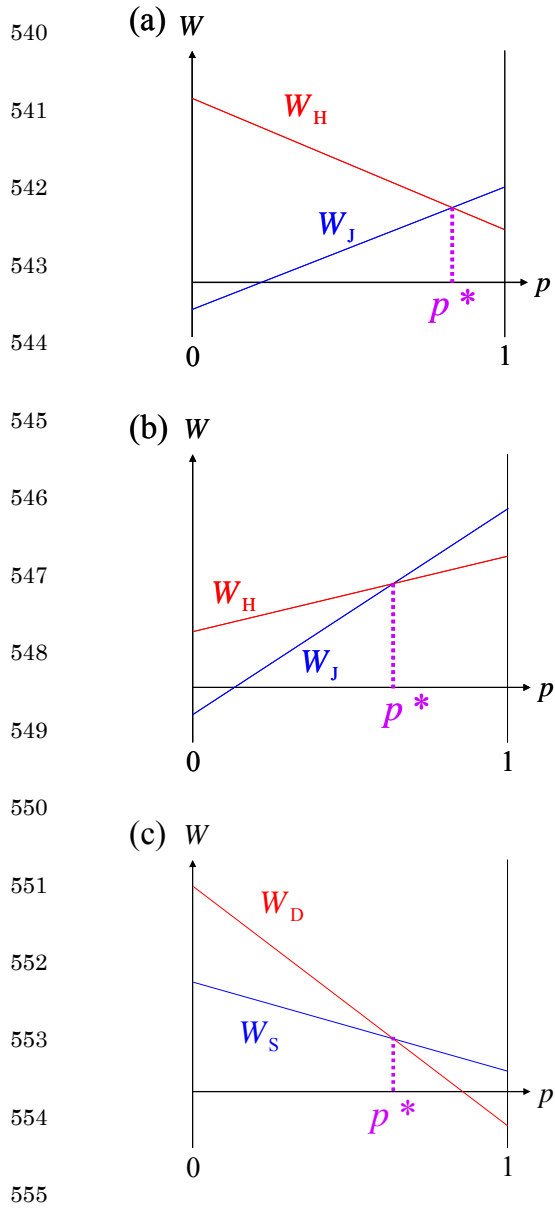
520 and subordinate, respectively.

521

Fig. 1

540

541

542

543

544

(a) *W*

W_H

W_J

$p*$

p

0   1

545

546

547

548

549

(b) *W*

W_H

W_J

$p*$

p

0   1

550

551

552

553

554

555

(c) *W*

W_D

W_S

$p*$

p

0   1

556   Fig. 2