Equilibria in Continuous Game of productive type:
Residual reproductive value and age-related dominance hierarchy

Takuya Kura, Nozomi Mizushima and Kenya Kura

Abstract

The residual reproductive value varies among individuals. This factor may affect animal contests, competitions, and dominance hierarchy. Using the same mathematical method developed in Kura & Kura (1998) and Kura (1999), we analyzed the relationship between the residual reproductive value and the investment level to the contests which directly affect reproduction. Our model can be regarded as a natural extension of the basic model in Maynard Smith (1982) and Maynard Smith & Brown (1986), where there is no evolutionary stable strategy (ESS) but unstable equilibrium. We found the unique pure ESS function in which a lower residual reproductive value induces a higher level of investment to contests. This stabilization of equilibrium is an important trait of a continuous game. For species in which an old animal has a lower residual reproductive value than a young animal after maturity, our conclusion predicts that the old animal has a heavier weapon than the young animal even if its body size is the same. For the same reason, an old animal should be less afraid to sustain a fatal wound, act more aggressively, and fight longer than a young animal. This may be the cause or preadaptation of the age-related dominance hierarchy system.

Introduction

In animal competition, many individual properties and conditions are more or less different from each other. Age is one of these. Although age does not directly affect animal contests, it may have indirect effects through the related traits such as body size, experience, and residual reproductive value. In the present paper, we focus on residual reproductive value and examine how it affects the animal contests, because many mathematical models have already dealt with the competition concerned with body size or resource holding potential (RHP) which includes experience as one factor (e.g., Rose, 1978; Hammerstein & Parker, 1982; Parker, 1983; Maynard Smith & Brown, 1986; Kura & Kura, 1998).

Since Fisher (1930) introduced the concept of "Reproductive value", many mathematical models concerning the best planning of life span have been proposed in

relation to the age or reproductive value (see Charlesworth [1994] and Roff [1992]). Many studies which dealt with the relationship between age and reproductive efforts concluded that after maturation, the reproductive efforts increase with age until almost close to the maximum life span (e.g., Gadgil & Bossert, 1970; Pianka & Parker, 1975; Charlesworth & León, 1976). In these studies, age and reproductive value are tightly linked. These studies dealt with the problem as an optimal problem of life history, and did not use game theoretical methods in a strict sense. Thus, their studies are not suitable for examining animal contests, where the reproductive success of each individual varies with the strategies other individuals adopt. In the present paper, using a similar mathematical method developed in Kura *et al*. (1997), Kura & Kura (1998) and Kura (1999), we consider a contest in which participants have different residual reproductive values from each other. For example, within species, some animals have a long life expectancy and others have a short life expectancy. The possession of the costly weapon or the mortal combat which leads to high mortality may be relative more costly for animals with a long life expectancy than for those with a short life expectancy. This may affect the arms level and the intention of contest. Furthermore, this model can be applied to contest situations in which larger ornaments of males are preferred by females and mortality is demanded to ensure honest signaling via viability costs.

The model

In our model, we assume that players compete for resources which are directly related with the reproduction. For example, males fight for the possession of females and the victor can copulate with the females, or individuals compete for territories where they copulate and nest to breed offspring. According to the models of Maynard Smith (1982) and Maynard Smith & Brown (1986), we assume that players decide the investment level m for the contest, and the return of the contest is determined by an individual's order of the investment level m from the lowest in the population, i.e., the probability that the investment level m of the individual is larger than that of a random opponent in the population. For instance, the order of the individual who invests highest is 1 and that of the individual who invests lowest is 0; the order is represented by the variable z. The investing level could represent arms or ornament size, willingness in a fatal fight, and so on. The function of the return from the contest is denoted by $V(z)$, which is a generally increasing non-linear function and is strictly

positive (Maynard Smith, 1982). Furthermore, we assume that $V(z)$ is a strictly monotonically increasing and differentiable function. We adopt the multiplicative model (Maynard Smith, 1982; Maynard Smith & Brown, 1986; Parker, 1983) in which the cost of the contest is mortality, and the total fitness is the product of survival and the fitness obtained if still alive after the contest. Let $s(m)$ be the viability of the individual whose investing level is m. Because a higher level of investment should incur a higher mortality, we should assume that $s(m)$ is continously differentialble, strictly dereaseing. We also assume that $s(m)$ tends to 0 as m approaches infinity, that is, when the level of investment becomes infinitely high, the viability converges to zero. The residual reproductive value after the contest when the individual would be still alive is denoted by a variable x. Strictly speaking, x is the residual reproductive value if the contest has not happened at all, but if it has happened, the residual reproductive value is $x+V(z)$ as below. The density function of the residual reproductive value is $p(x)$ (>0) which is defined on the domain $[0, a]$. We do not assume other differences among players such as the resource holding potential (RHP) difference in competition in Kura & Kura (1998) or the resource value difference in Kura *et al.* (1997). W_x denotes the expected total fitness of the individual whose residual reproductive value is x, investment level is m, and the order of the investment level is z, then we get

$$W_x = s(m)\{x+V(z)\}. \tag{1}$$

The animal should maximize this W_x. Note that In this model, the fitness function is productive type. In contrast, that of models in Kura *et al.* (1997), Kura & Kura (1998), Kura (1999) is fundamentally additive type.

　　When the residual reproductive value of a player is x, his strategy is regarded as the level function of investment $M(x)$. Assuming that $M^*(\bullet)$ occupies a population, when a player employs a strategy of level of investment m on a point where his residual reproductive value is x, his expected total fitness is denoted by $W_x(m, M^*)$. The definitions of a pure ESS function and a symmetric Nash equilibrium strictly follow Kura *et al.* (1997) and Kura & Kura (1998), that is, for all x and all m ($\neq M^*(x)$), function $M^*(\bullet)$ is a pure ESS function when $W_x(m, M^*) < W_x(M(x), M^*)$, and $M^*(\bullet)$ is a (symmetrical) Nash equilibrium when $W_x(m, M^*) \leq W_x(M(x), M^*)$. In this definition, a pure ESS function is necessarily a Nash equilibrium function.

　　When a strategy $M^*(\bullet)$ occupies the population, the variable z, the average order of the investment level m in the population, is regarded as a function of m and $M^*(\bullet)$

and denoted by $z(m, M^*)$. For convenience, the return of the contest also is denoted by

$$U(m, M^*) = V(z(m, M^*)). \tag{2}$$

Analysis

In this section, we seek for a pure ESS function and a Nash equilibrium function in the class of differentiable function. In fact, by using almost the same mathematical technique as that used by Kura & Kura (1998), we can prove that a Nash equilibrium function is differentiable. Because this proof is highly mathematical and less important, it is not shown here. We can also prove that a Nash equilibrium function is strictly monotonically decreasing. The proof is shown in Appendix A because from the mathematical viewpoint, monotonicity is essential in our method, and differentiability follows it (Kura *et al.*, 1997; Kura & Kura, 1998).

First, let us seek conditions under which $M^*(\bullet)$ would be a Nash-equilibrium function. Suppose that $M^*(\bullet)$ which is a strictly monotonically decreasing differentiable function occupies a population, from (1) and (2), we have

$$W_x(m, M^*) = s(m)\{x + U(m, M^*)\}. \tag{3}$$

Suppose that $M^*(\bullet)$ is a Nash equilibrium function. When x and $M^*(\bullet)$ are fixed and m is varied, from definition, (3) should take the maximum when $m = M^*(x)$. Now, we should consider the relevant range of m only as the closure of $M^*(\bullet)$'s range and $(m=)0$. This is because if m is smaller than the $M^*(\bullet)$'s range, it can not win. If m is greater than the $M^*(\bullet)$'s range, which is bounded by β, its payoff can not be greater than $(m=)\beta$. Then, there always exists an inverse function $u(\bullet)$ for a strictly monotonically continuous function $M^*(\bullet)$ on the range of $M^*(\bullet)$. Hence, we specify x^* such that $M^*(x^*) = m$, that is, $u(m) = x^*$.

Because of differentiability, $W_x(m, M^*)$ has to be greatest when $m = M^*(x)$ with respect to first variable m. This implies that the derivative of (3) should be 0, that is,

$$\partial W_x(m, M^*)/\partial m|_{m=M^*(x)} = s'(M^*(x))\{x + U(M^*(x), M^*)\}$$
$$+ s(M^*(x))V'(z^*)p(u(M^*(x)))/M^{*'}(x)$$
$$= 0, \tag{4}$$

where $z^* = z(M^*(x), M^*)$.

Because $M^*(\bullet)$ is monotonically decreasing, an individual with the largest residual reproductive value α never wins and any level of investment would be a waste. Hence, the level of investment $M^*(\alpha)$ is 0. Since this becomes the initial value of differential equation (4), the candidate for a Nash-equilibrium solution of (4) is unique. However, it is only a necessary condition for $M^*(\bullet)$ to satisfy differential equation (4). Let us next show that equation (4) is also a sufficient condition for a Nash equilibrium, and more strictly, it is also the condition for a pure ESS function.

From definition, for all x, if $W_x(m, M^*)$ takes the unique highest value with respect to the first variable when $m = M^*(x)$, $M^*(\bullet)$ is a pure ESS function. This is a sufficient condition, and if $M^*(\bullet)$ satisfies (4), it also satisfies this condition as follows;

Substituting $x = x^*$ and $M^*(x) = m$ to (4), we have

$$\partial W_x{}^*(m, M^*)/\partial m$$
$$= s'(m)\{x^* + U(m, M^*)\} + s(m)V'(z)p(u(m))/M^{*'}(x^*) = 0, \tag{5}$$

where $z = z(m, M^*)$. Generally, it is

$$\partial W_x(m, M^*)/\partial m = s'(m)\{x + U(m, M^*)\} + s(m)V'(z)p(u(m))/M^{*'}(x^*)$$

from (5),

$$= s'(m)\{x + U(m, M^*)\} - s'(m)\{x^* + U(m, M^*)\}$$
$$= s'(m)\{x - x^*\}. \tag{6}$$

Since $M^*(\bullet)$ is monotonically decreasing and $s'(m) < 0$, $\partial W_x(m, M^*)/\partial m$ is positive when $m = M^*(x^*) < M^*(x)$ (that is $x^* > x$), and it is negative when $m > M^*(x)$ (that is $x^* < x$). This implies that $W_x(m, M^*)$ takes the unique highest value when $m = M^*(x)$. Hence, the solution of (4) is concluded to be a pure ESS function.

At last, let us illustrate an example by assuming more concrete functions. When $p(\nu)$ is a uniform distribution defined on $[0,1]$ that is $p(\nu) = 1$ $(0 \leq \nu \leq 1)$, $s(m) = \exp(-m)$, and $V(z) = z$, differential equation (4) becomes

$$-\exp(-M^*(x))\{x+M^*(x)+1/M^{*\prime}(x)\}=0. \tag{7}$$

Because the initial value of (7) is $M^*(1)=0$, the solution of (7) is

$$M^*(x)=1-x.$$

This is the unique pure ESS function, and it is obvious that this is strictly monotonically decreasing.

Discussion

As Mentioned in section 2, the above game is a natural extension of the basic game of arms race proposed by Maynard Smith (1982) and Maynard Smith & Brown (1986). The basic game has no ESS but an unstable equilibrium. Then they supposed that unstable escalation is an essential trait of the model, and many variations of minor change have been studied to seek stable equilibria (Parker, 1983; Maynard Smith & Brown, 1986). However, in the strict sense, there must exist more or less a difference in residual reproductive value among animals. Hence, the game in our model is one of the most natural extensions of the basic game, and there is a unique ESS function, that is, stable equilibrium. Moreover, using the same mathematical method as that developed by Kura & Kura (1998) and Kura (1999), we can prove that when the difference of residual reproductive value among players become smaller to zero, the pure ESS function in this game converses to the unstable equilibrium of the basic game which does not assume individual differences. This change of traits of equilibrium is a stabilization of equilibrium by adding one more parameter of players to original game. This kind of stabilization of equilibrium has been also found in all-pay games in Kura (1999). These findings shed a new light on the concept about stability of equilibrium in game theory.

We currently assume that the distribution of residual reproductive value $p(\bullet)$ and the strategy function of all players $M(\bullet)$ is independent. However, there is an interaction. If more fighting goes, that is, $M(\bullet)$ becomes higher, this would reduce survival of animals and change $p(\bullet)$. Ideally, we would like to solve a complete life-history game where residual reproductive value is derived through survival values, which are in turn affected by $M(x)$. However, this extension might be too ambitious

for the current purpose and too difficult to solve.

While there is such limitation, the above model shows that an individual who has a lower residual reproductive value should invest more in contests which are directly related with immediate reproduction. For simplification, an individual who has less hope of future reproduction should be less afraid to die and should stake more to the current contest.

After maturity, the residual reproductive value generally decreases with age. Our model thus predicts that an old animal has a heavier weapon or a larger sexual ornament than a young one even if the body size is the same. For instance, the antlers of Cervidae may be suitable to test this hypothesis because antlers are generally renewed each year in this family. Indeed, several authors found that antler size or the complexity of the male still develops greatly after maturation except when they get so old that they rarely survive (Blood & Lovaas, 1966; Wolfe, 1982; Hartl *et al.*, 1995). Hayden *et al.* (1994) studied antler growth and morphology in a feral sika deer (*Cervus nippon*) population in Ireland. Although, they did not test for statistical significance, it seems that in comparison with the body size, the antler size grew with age after maturation. Another possible example is the Asian Paradise Flycatcher (*Terpsiphone paradisi*), which is a sexually dimorphic bird, and adult males have tails more than two times as long as the body length. In this species, the male lengthen its tail with age after maturation (Mizuta & Yamagishi, 1998; Mizuta, Personal communications).

There is another way to test the prediction that the old animal is less afraid of death than the young or middle-aged animal. Many animals have strong weapons, and their fights may often fatally wound one of them. Even if for animals not having strong arms, battles between them may attract predators and a long battle may increase the risk of predation. In this case, old animals should also perform longer and more boisterous fights than young animals. We also suggest that this prediction is an important factor in the age-related dominance hierarchy system.

The age-related dominance hierarchy system or in a broader sense, age-related dominance phenomenon which implies that age and dominance are positively correlated in a population is observed in many animal species, for example, the queenless ponerine ant, (*Pachycondyla sublaevis*) (Higashi, *et al*, 1994), the Japanese paper wasp (*Polistes chinensis antennalis*) (Miyano, 1986), the boat-tailed grackle (*Quiscalus major*) (Post, 1992), swallow-tailed manakin (*Chiroxiphia caudata*) (Foster, 1981), long-tailed manakin (*Chiroxiphia linearis*) (McDonald, 1989), gray

squirrel (*Sciurus carolinensis*) (Pack *et al.*, 1967; Allen & Aspey, 1986), Japanese macaque (*Macaca fuscata*)(Johnson *et al.*, 1982), and the Cretan agrimi (*Capra aegagrus cretensis*) (Husband & Davis, 1984). Especially, McDonald (1989) observed the long-tailed manakin, which is a lekking bird, and found a strict dominance hierarchy in spite of a weight decrease with age. In gulls, old pairs tend to occupy a good nesting site (Pugesek, 1981; Reid, 1988). In some spices of wasps, it is well known that age and dominance are positively correlated among workers in spite that workers who were born early are usually smaller than later born workers (e.g., Hughes & Strassmann, 1988; O'Donnell & Jeanne, 1995).

Because most mammals and birds do not grow after maturation, there is an overt question concerning age-related dominance hierarchy: Why do not young individuals who are bigger or have a higher RHP challenge the dominant individual by fight and why are they willing to follow the hierarchy? Wiley & Rabenold (1984) studied birds which have helpers and argued that the reason is a kind of delayed reciprocity, that is "The young that an individual helps to raise become the individual's helpers when it succeeds to breeding status in the group". However, we do not agree that such a kind of reciprocity is evolutionary stable because the receiver of "reciprocity" is not the same individual as the sender of it. Moreover, their explanation can be applied only to species with a helper, and can be hardly applied to species such as lekking birds (McDonald, 1989). Instead, we suggest that age-related dominance hierarchy, at least, in the early stage of its evolution, is based on the aggressiveness or bravery related with the residual reproductive value.

The residual reproductive value of a male is not strongly related to the genetic quality of the male. Therefore, if the male with a low residual reproductive value tends to win a fight and attains a dominant rank as mentioned above, the female would not necessarily have to prefer a higher ranking individual. This gap between dominant rank and female preference gives rise to a conflict between dominant males and females, and consequently obscures the relationship between rank-order and reproductive success. For example, in Japanese macaque (*Macaca fuscata*), there is a strong correlation between male social rank and age (Johnson *et al.*, 1982), but females do not particularly prefer high-ranking males. They rather prefer middle-ranking young adult males (Takahata, 1982; Huffman, 1992). (Old mate preference is theoretically analyzed by Hansen & Price [1995], Kokko [1997] and Kokko & Lindström [1996]).

There is an argument that the living being which has a finite life span should

increase reproductive efforts with age (Gadgil & Bossert, 1970; Pianka & Parker, 1975; Charlesworth & León, 1976). This is called "residual reproductive value hypothesis", but the empirical results do not sufficiently support this hypothesis (Pianka & Parker, 1975; Clutton-Brock, 1984; Reid, 1988; Perdeck & Cavé, 1992; but see Pugesek, 1981). Although our hypothesis is a sort of "residual reproductive value hypothesis", there is a critical difference between previous discussion and here. Direct reproductive efforts such as egg number and parental care which ware discussed in previous papers may be strongly restricted by physical or ecological environments, and animals can not easily increase them, that is, the marginal utility of the effort rapidly decreases in comparison with increasing mortality. In contrast, animal contests are purely social traits and weakly restricted by physical or ecological environments. Then, if an individual bids his mortality to a contest, the result may be proportional to the bid. Hence, we suppose that the investment of contest or sexual advertisement is more strongly related to residual reproductive value than the direct reproductive efforts.

In the present paper, we did not take into account the RHP difference in competition such as mentioned by Kura & Kura (1998). It is possible, however, that the RHP decreases with age in some cases. Because a low RHP leads to less attrition time (Kura & Kura, 1998) and a low armed level or sexual advertisement (Kura, 1999), decrease in the RHP with age affects inversely the relationship between age and winning probability of contests. In addition, the reproductive value of an immature individual is less than that of an adult in general. However, an immature individual is also small in body size, and has a low RHP. Therefore, immature animals may reluctantly obey dominance hierarchies in many species. We hope field researchers will note the above predictions and examine whether they are true or not.

REFERENCES

Allen, D.S. & W. P. Aspey, 1986 "Determinants of social dominance in eastern gray squirrels (*Sciurus carolinensis*): A quantitative assessment" *Anim Behav.*, Vol. 34, pp. 81-89.

Blood, D.A. & A.L. Lovaas, 1966 "Measurements and weight relationships in Manitoba elk" *J .Wildl. Manage.*, Vol. 30, pp. 135-140.

Charlesworth, B. 1994 *Evolution in Age-structured Populations. 2nd edn.* Cambridge: Cambridge University Press.

Charlesworth, B. &J.A. León, 1976 "The relation of reproductive effort to age" *Am. Nat.*, Vol. 110, pp. 449-459.

Clutton-Brock, T.H. 1984 "Reproductive effort and terminal investment in iteroparous animals" *Am. Nat.*, Vol. 123, pp. 212-229.

Fisher, R.A. 1930 *The Genetical Theory of Natural Selection.* Oxford: Clarendon Press.

Foster, M.S. 1981 "Cooperative behavior and social organization of the swallow-tailed manakin "(*Chiroxiphia caudata*). Behav. Ecol. Sociobiol., Vol. 9, pp. 167-177.

Gadgil, M. & W.H. Bossert, 1970 "Life historical consequences of natural selection" *Am. Nat.*, Vol. 104, pp. 1-24.

Hartl, G.B., F. Klein, R. Willing, M. Apollonio, & G. Lang, 1995 "Allozymes and the genetics of antler development in red deer (*Cervus elaphus*)" *J. Zool.,*(*Lond.*) Vol. 237, pp. 83-100.

Hammerstein, P. & G.A. Parker, 1982 "The asymmetric war of attrition" *J. theor. Biol.*, Vol. 96, pp. 647-682.

Hansen, T.F. & D.K. Price, 1995 "Good genes and old age: Do old mates provide superior genes?" *J. Evol. Biol.*, Vol. 8, pp. 759-778.

Hayden, T.J., J.M. Lynch, & G. O'Corry-Crowe, 1994 "Antler growth and morphology in a feral sika deer (*Cervus nippon*) population in Killarney, Ireland" *J. Zool.,* (*Lond.*) Vol. 232, pp. 21-35.

Higashi, S., F. Ito, N. Sugiura, & K. Ohkawara, 1994 "Worker's age regulates the linear dominance hierarchy in the queenless ponerine ant *Pachycondyla sublaevis* (Hymenoptera: Formicidae)" *Anim. Behav.*, Vol. 47, pp. 179-184.

Huffman, M.A. 1992 "Influences of female partner preference on potential reproductive outcome in Japanese macaques" *Fol. Primatol.*, Vol. 59, pp. 77-88.

Hughes, C. R. & J.E. Strassmann, 1988 "Age is more important than size in determining dominance among workers in the primitively eusocial wasp, Polistes

instabilis" *Behaviour* Vol. 107, pp. 1-14.

Husband, T.P. & P.B. Davis, 1984 "Ecology and behavior of the Cretan agrimi" *Can. J. Zool.*, Vol. 62, pp. 411-420.

Johnson, D.F., K.B. Modahl, & G.G. Eaton, 1982 "Dominance status of adult male Japanese macaques (*Macaca fuscata*) : Relationship to female dominance status, male mating behavior, seasonal changes and developmental changes" *Anim. Behav.*, Vol. 30, pp. 383-392.

Kokko, H. 1997 "Evolutionarily stable strategies of age-dependent sexual advertisement" *Behav. Ecol. Sociobiol.*, Vol. 41, pp. 99-107.

Kokko, H. & J. Lindström 1996 "Evolution of female preference of old mates" *Proc. R. Soc. Lond. B.*, Vol. 263, pp. 1533-1538.

Kura,T. 1999 "Dilemma of the equality : An all-pay contest with individual differences in resource holding potential" *J. theor. Biol.*, Vol. 198, pp. 395-404.

Kura, T. & K. Kura, 1998 "War of attrition with individual differences on RHP" *J. theor. Biol.*, Vol. 193, pp. 335-344.

Kura T, K. Kura, & T. Shichijo, 1997 "The law of payoff consistency: Games with continuous differences on resource values" *J. Ethol.*, Vol. 15, pp. 95-101.

Maynard Smith, J. 1982 *Evolution and Theory of Games*. Cambridge: Cambridge University Press.

Maynard Smith, J. & R. L. W. Brown, 1986 "Competition and body size" *Theor. Pop. Biol.*, Vol. 30, pp. 66-179.

McDonald, D.B. 1989 "Cooperation under sexual selection: Age-graded changes in a lekking bird" *Am. Nat.*, Vol. 134, pp. 709-730.

Miyano, S. 1986 "Colony development, worker behavior and male production in orphan colonies of a Japanese paper wasp *Polistes chinensis antennalis* Pérez (Hymenoptera: Vespidae)" *Res. Popul. Ecol.*, Vol. 28, pp. 347-367.

Mizuta, T. & S. Yamagishi 1998 "Breeding biology of monogamous Asian Paradise Flycatcher *Terpsiphone paradisi* (Aves: Monarchinae): a special reference to colour dimorphism and exaggerated long tails in male" *Raffles Bull. Zool.*, Vol. 46, pp. 101-112.

O'Donnell, S. & R.L. Jeanne, 1995 "The roles of body size and dominance in division of labor among workers of the eusocial wasp *Polybia occidentalis* (Olivier) (Hymenoptera: Vespidae)" *J. Kans. Entomol. Soc.*, Vol. 68, pp. 43-50.

Pack, J.C., H.S. Mosby, & P.B. Siegel 1967 "Influence of social hierarchy on gray squirrel behavior" *J. Wildl. Manage.*, Vol. 31, pp. 720-728.

Parker,G.A. 1983 "Arms races in evolution - An ESS to the opponent-independent costs game" *J. theor. Biol.*, Vol. 101, pp. 619-648.

Perdeck, A.C. & A.J. Cavé, 1992 "Laying date in the coot: Effects of age and mate choice" *J. Anim. Ecol.*, Vol. 61, pp. 13-19.

Pianka, E.R. & W.S. Parker, 1975 "Age-specific reproductive tactics" *Am. Nat.*, Vol. 109, pp. 453-464.

Post, W. 1992 "Dominance and mating success in male boat-tailed grackles" *Anim. Behav.*, Vol. 44, pp. 917-929.

Pugesek, B.H. 1981 "Increased reproductive effort with age in the California gull (*Larus californicus*)" *Science*, Vol. 212, pp. 822-823.

Reid, W.V. 1988 "Age-specific patterns of reproduction in the glaucous-winged gull: Increased effort with age ?" *Ecology*, Vol. 69, pp. 1454-1465.

Roff, D.A. 1992 *The Evolution of Life Histories : Theory and Analysis*. New York: Chapman & Hall.

Rose, M.R. 1978 "Cheating in evolutionary games" *J. theor. Biol.*, Vol. 75, pp. 21-34.

Takahata, Y. 1982 "The socio-sexual behavior of Japanese monkeys. *Z. Tierpsychol.*, Vol. 59, pp. 89-108.

Wiley, R.H. & K.N. Rabenold, 1984 "The evolution of cooperative breeding by delayed reciprocity and queuing for favorable social positions" *Evolution*, Vol. 38, pp. 609-621.

Wolfe, G. J. 1982 "The relationship between age and antler development in Wapiti" In : *Antler Development in Cervidae*. (Brown, R.D., ed) pp.29-36. Kingsville,TX: Caesar Kleberg Wildlife Research Institute.

Appendix

Theorem

Suppose that a Lebesgue measurable function $M^*(\bullet)$ is a Nash-equilibrium in this game. Then $M^*(\bullet)$ is strictly monotonically decreasing.

Proof

Choose x_1 and x_2 such that $x_1 < x_2$ and denote $m_1 = M^*(x_1)$, $m_2 = M^*(x_2)$. Because $M^*(\bullet)$ is a Nash-equilibrium function, $W_{x1}(m_1, M^*) \geq W_{x1}(m_2, M^*)$ and $W_{x2}(m_2, M^*) \geq W_{x2}(m_1, M^*)$. Then

$$
\begin{aligned}
0 \leq &W_{x1}(m_1, M^*) - W_{x1}(m_2, M^*) + W_{x2}(m_2, M^*) - W_{x2}(m_1, M^*) \\
&= s(m_1)\{x_1 + U(m_1, M^*)\} - s(m_2)\{x_1 + U(m_2, M^*)\} \\
&\quad + s(m_2)\{x_2 + U(m_2, M^*)\} - s(m_1)\{x_2 + U(m_1, M^*)\} \\
&= \{s(m_1) - s(m_2)\}\{x_1 \text{-} x_2\}.
\end{aligned} \tag{A.1}
$$

Because $x_1 < x_2$ and $s(\bullet)$ is decreasing, the above inequality implies $s(m_1) - s(m_2) \leq 0$, then $m_1 = M^*(x_1) \geq m_2 = M^*(x_2)$, that is, $M^*(\bullet)$ is decreasing.

It is also obvious that $M^*(x_1) > M^*(x_2)$. Because if $M^*(x_1) = M^*(x_2)$, then for all x $(x_1 \leq x \leq x_2)$, $M^*(x) = M^*(x_1) = m_1$. This implies that there is a non-zero measure of the players whose investment level is strictly m_1. Then if we take sufficiently small $\varepsilon > 0$, since there is a gap between $z(m + \varepsilon, M^*)$ and $z(m, M^*)$, but not between $s(m_1 + \varepsilon)$ and $s(m_1)$, we obtain

$$
\begin{aligned}
W_{x1}(m_1 + \varepsilon, M^*) &= s(m_1 + \varepsilon)\{x_1 + V(z(m + \varepsilon, M^*))\} \\
&> s(m_1)\{x_1 + V(z(m, M^*))\} = W_{x1}(m_1, M^*).
\end{aligned}
$$

This contradicts with the assumption that $M^*(\bullet)$ is a Nash-equilibrium function.