行政院國家科學委員會補助專題研究計畫成果報告

※ ※※※※※※※※※※※※※※※※※※※※※※※※※

※ **福山魚怪的生活史及性轉變** (2/2) ※

※※※※※※※※※※※※※※※※※※※※※※※※※

計畫類別：■個別型計畫　　□整合型計畫

計畫編號：NSC89-2311-B-002-081

執行期間：　89 **年** 8 **月** 1 **日至** 90 **年**　7 **月** 31 **日**

計畫主持人：戴昌鳳

本成果報告包括以下應繳交之附件：

□赴國外出差或研習心得報告一份

□赴大陸地區出差或研習心得報告一份

□出席國際學術會議心得報告及發表之論文各一份

□國際合作研究計畫國外研究報告書一份

執行單位：台灣大學海洋研究所

中　華　民　國　　90　**年**　10　**月**　25　**日**

行政院國家科學委員會專題研究計畫研究成果報告

福山魚怪的生活史及性轉變 (2/2)

Life history and sex change of *Ichthyoxenus fushanensis* (2/2)

計畫編號:NSC89-2311-B-002-081

執行期間:89 **年** 8 **月** 1 **日至** 90 **年** 7 **月** 31 **日**

計畫主持人: **戴昌鳳　台灣大學海洋究所**

計畫參與人員：蔡明利、呂麗娟、何瓊紋　台灣大學海洋研究所

一、 中文摘要

福山魚怪的生活史中具有二種性別間殘食現象。其一是雌性個體於交配後攝食雄性個體，通常稱為性殘食；另一為雄性個體攝食雌性個體，我們稱為反性殘食。二種殘食現象皆發生於生殖季節(四至十一月)，其中，性殘食發生於生殖季初期，反性殘食則發生於生殖季後期。此外，二種殘食現象皆發生於寄主體長小於十公分，且雌雄體長比例小於 1.6, **而在殘食之後, 雌雄的體長比例迅速增大。我們認為這種殘食現象是生物在資源不足情況下的特殊適應；雌性生殖季初期攝食較小的雄性，可以獲得能量用於生殖；而在生殖季後期，雌性已無生殖潛能，此時雄性攝食雌性，並迅速增長及變性。因此，兩者皆是經濟性的殘食現象。**

關鍵字: **福山魚怪，生活史，性轉變**

二、 英文摘要

Two types of inter-sexual cannibalism, based on the sex victim, were detected between heterosexual pairs of the parasitic isopod, *Ichthyoxenus fushanensis*, residing in the body cavity of the freshwater fish, *Varicorhinus bacbatulus*. One type was regarded as sexual cannibalism in which the male was consumed by the female before or after mating. Another was a reversed type in which the female was eaten by her mate during or after breeding. Both types of cannibalism occurred during the breeding season from April to November, with the female-on-male cannibalism occurring at earlier stages, and the reversed type occurring later. The availability of juveniles in the breeding season may ensure that a mating pair is formed immediately after the cannibalism occurs. Both types of cannibalism occurred in those pairs inhabiting smaller hosts (< 10 cm in body size) suggesting that resource limitation is possibly an important factor triggering the cannibalism. Cannibalism may lead to rapid growth or sex change of the cannibal. Both types of cannibalism occurred in mating pairs with a smaller size ratio (below 1.6, female to male), and both resulted in a great departure of female size from its mate. The increase in size ratio between paired individuals ultimately leads to an increase of clutch size. Since an individual of *I. fushanensis* may potentially display both male and female functions by undergoing protandrous sex

change, the cannibalistic behavior would not have evolved in response to selection on either male or female. Both types of cannibalism may be regarded as the result of competition between paired individuals, which is a by-product in the evolution of a reproductive strategy rather than the consequence of sexual selection.

Keywords: *Ichthyoxenus fushanensis*, parasitism, sex change, selection

三、 計畫緣由與目的

Sexual cannibalism, as defined by Elgar (1992), is the consumption of a male by a female at some stage of courtship or copulation or immediately thereafter. It occurs in many spiders and scorpions, opisthobranchs, amphipods, copepods, and in three orders of insects (Polis 1981, Buskirk et al. 1984, Elgar 1992, Arnqvist and Henriksson 1997). The term 'sexual cannibalism' can be misleading as it masks important differences between 'economic' and 'sacrificial' cannibalism (Peretti and Acosta 1999). Selection for economic cannibalism is based on what is optimal for females (Newman and Elgar 1991), and this can explain pre-copulatory cannibalism in spiders. Obviously, it is never optimal for a male to be eaten by a female before sperm transfer, so such cannibalism reflects greater female power in the 'conflict of interest' (Peretti and Acosta 1999). On the other hand, selection for sacrificial cannibalism has been shown to have two paternity advantages: cannibalized males fertilize more eggs than do on-cannibalized males, and females are less likely to remate following consumption of their first mate (Andrade 1996). Therefore, sexual cannibalism may represent two routes to its evolution. First, from a female's point of view, if the risks involved in cannibalizing males are slight, and males are sufficiently common, then any particular male may have more value as a meal than a mate. Second, if a male is unlikely to survive to mate with another female, and, by self-sacrifice he increases the fitness of his offspring (through greater provisioning, for example) it may be favored (Buskirk et al. 1984, Andrade 1996). The costs and benefits on male and female fitness have been examined theoretically and empirically (Buskirk et al. 1984, Newman and Elgar 1991, Arnqvist and Henriksson 1997).

A flesh-burrowing protandrous parasite, *Ichthyoxenus fushanensis* was found residing in the body cavity of a freshwater fish, *Varicorhinus bacbatulus* (Tsai and Dai 1999). The isopods, often in heterosexual pairs, live in a membranous sac of the host fish adjacent to the pectoral fin. Due to the very low transmission rate, selection favors large and productive females to compensate for the mass mortality of juveniles (Tsai et al. 1999). Selection favors the more productive combination of a larger female and a smaller male. However, how such a productive mating system can be achieved remains unanswered. Here we describe two types of inter-sexual cannibalism in the protandrous isopod *I. fushanensis* and provide evidence to address questions of how cannibalistic behavior may influence the performance of the mating system.

四、 材料及方法

Infected fish of *Varicorhinus bacbatulus* were collected biweekly from spring 1998 to summer 2000 in upstream sections of Nanshih Stream, a fast running stream located in a mountainous area of northern Taiwan. The fish infected by *Ichthyoxenus fushanensis* were easy to distinguish by the existence of an orifice near the pectoral fin. All infected fish were brought to the laboratory alive.

Each of the infected fish was cultured separately in a 35 x 45-cm aquarium with a filter and air supply system. *Ichthyoxenus fushanensis* in the hosts may contain embryos at different developmental stages that could not be examined from the exterior of the host fish. After the first juvenile was released from the orifice, the host fish was dissected. Then individuals of *I. fushanensis* were removed from the parasitic sac, and the body lengths of both hosts and parasitic isopods were measured in millimeters. A water jet was used to remove juveniles from the brood pouch of the female, and the number of juveniles was counted to represent clutch size. After one week, those fish that did not release juveniles of the parasites were also dissected.

After dissection, the content of the parasitic sac of infected fish was carefully examined. The pair with one individual eating its mate or with an incomplete fresh body and a cannibal was recognized as a positive case of cannibalism. In some cases, it was easy to identify from the orifice, especially when the male was the victim, because the male is always located near the opening of the orifice.

In order to determine whether the cannibalism occurred before or after copulation, the brooding of a single female was monitored. After the fragment of a male victim was removed from the orifice carefully, the female isopod who was cannibalizing her mate was cultured with six host fish separately in a tank without a new mate for 3 months. Juveniles released by the female indicated that the cannibalistic behavior occurred during or after courtship.

五、 結果及討論

A total of 29 cases of cannibalism were found in paired *Ichthyoxenus fushanensis*. These instances of cannibalisms could be classified into 2 types based on the sex of the cannibals. In 12 cases, females preyed on males, and this was recognized as a case of sexual cannibalism. Another 17 cases were the reversed type of sexual cannibalism in which females were consumed by males. In these cases, the residual fresh body of a female was found to contain a few living juveniles or empty oostegites, indicating that the cannibalism occurred during or after the release of juveniles. In addition, a few cases consisting of a brooding female and an immature individual were found indicating that the original mate of the female had been replaced.

In 6 of the 12 cases of sexual cannibalism, the hosts were cultured separately after the debris of the male was carefully removed from the orifices. During the following 3 months, 4 cases showed that a female releasing juveniles. This indicates that the cannibalism may have occurred before, during, or after the copulation. This is consistent with the definition of sexual cannibalism in which the male is consumed by the female before, during, or immediately after courtship or copulation (Elgar and Crespi, 1992).

Both types of cannibalism of *Ichthyoxenus fushanensis* took place during the breeding season from April to November when free-living juveniles were available (Fig. 1). The female-on-male cannibalism mainly occurred at early stages and the male-on-female cannibalism at late stages of the breeding season (Fig. 1). In addition, all cases of cannibalism between pairs of *I. fushanensis* occurred where the host body size was less than 10 cm (Fig. 2), and the body size ratios (female/male parasites) were below 1.6 (Table 1). However, when a new juvenile entered the parasitic sac, the size ratio of the new pair might be greatly increased (Table 1).

In natural pairs, the body size of the

female is always larger than that of her mate. However, body size distributions of the two sexes overlapped (Fig. 3). During the breeding season, females were often 1.6 times larger than the paired males (Fig. 4). The distribution of size ratios (female to male) of 87 brooding pairs showed one major peak at 2.5 and a minor peak at 1.6 (Fig. 4). This indicates that two types of combination may exist and a rapid shift of size ratios may have occurred in the mating system.

The size ratio of the paired female and male at reproduction displayed a significant positive relationship with clutch size (Table 2a). The size ratio was, however, positively related to host body size ($r = 0.706$, $p < 0.001$; Table 2a) and female size ($r = 0.865$, $p < 0.001$), and clutch size was also closely related to female size at reproduction ($r = 0.987$, $p < 0.001$; Table 2a). Thus, the relationship between size ratio and clutch size might be masked by these dependent variables (host size and female size). In order to obtain the actual correlation between the size ratio of paired sexes and clutch size, the influences of other dependent variables (e.g., host size, female size) were eliminated. When the effect of host size was removed, both the absolute and relative clutch sizes were significantly related to the size ratio of the paired female to male (Table 2b; Fig. 5). This indicates that mating pairs with larger size ratios are a more productive combination, and that the size ratio may, either directly or indirectly, influences the number of young being released.

六、參考文獻

Andrade, M. C. B. 1996. Sexual selection for male sacrifice in the Australian redback spider. - Science 271: 70-73.

Elgar, M. A. and Fahey, B. F. 1995. Sexual cannibalism, competition, and size dimorphism in the orb-weaving spider *Nephila plumipes* Latreille (Araneae: Araneoidea). – Behav. Ecol. **7:** 196-198.

Elgar, M. A. and Nash, D. R. 1988. Sexual cannibalism in the garden spider *Araneus diadematus*. – Anim. Behav. 36: 1511-1517.

Fox, L. R. 1975. Cannibalism in natural populations. – Annu. Rev. Ecol. Syst. 6: 87-106.

Tsai, M. L. and Dai, C. F. 1999. *Ichthyoxenus fushanensis,* new species (Isopoda: Cymothoidae) parasite of the freshwater fish, *Varicorhinus bacbatulus,* from northern Taiwan. – J. Crust. Biol. 19**:** 917-923.

Tsai, M. L., Li, J. J. and Dai, C. F. 1999. Why selection favors protandrous sex change for *Ichthyoxenus fushanensis*? – Evol. Ecol. 13: 327-338.

Tsai, M. L., Li, J. J. and Dai, C. F. 2001. How host size may constraint the evolution of parasite body size and clutch size? The parasitic isopod, *Ichthyoxenus fushanensis* and its host fish, *Varicorhinus bacbatulus,* as an example. - Oikos 92: 13-19.

Twombly, S. and Tisch, N. 2000. Body size regulation in copepod crustaceans. - Oecologia 122**:** 318-326.

Wagner, J. D. and Wise, D. 1996. Cannibalism regulates densities of young wolf spiders: evidence from field and laboratory experiments. - Ecology 77: 639-652.

Wickman, P. O. and Karlsson, B. 1989. Abdomen size, body size and the reproductive effort of insect. - Oikos 56: 209-214.

p.s. The full paper of this manuscript has been submitted to *Oikos*.