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Age-related reproductive biology of *Trichogrammatoidea lutea* on eggs of the African bollworm *Helicoverpa armigera*

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Abstract

Trichogrammatoidea lutea Girault (Hymenoptera Trichogrammatidae) is an egg parasitoid of the African bollworm *Helicoverpa armigera* (Hubner) (Lepidoptera Noctuidae) in southern Africa. To determine the potential of *T. lutea* as a biological control agent of *H. armigera*, longevity, daily parasitism, fecundity, number of progeny per egg and sex ratio with regard to maternal age were examined under laboratory. The maximum longevity of *T. lutea* male and female adults was 14 and 16 days, respectively. Reproduction by *T. lutea* commenced on the day of eclosion and lasted for 14 days. The mean realized fecundity of *T. lutea* was 52 offspring per female. Daily fecundity and sex allocation depended on maternal age. Daily percentage parasitism and fecundity were highest on the day of eclosion and decreased with female age until no egg was parasitized from day 15. The sex ratio was female-biased during the first three days, and thereafter became male-biased from day 4 until day 14. The number of progeny per host egg was also highest at 2.2 on the day of eclosion, then decreased to 0.9 on day 8 and thereafter increased to 2.0 on day 13. The overall sex ratio of *T. lutea* was approximately 1:1. The net replacement rate (R_0), mean generation time (T) and intrinsic rate of population increase (r_m) of *T. lutea* were determined at 25.5, 9.8 and 0.3, respectively. Findings from this study show great potential of *T. lutea* as a biological control agent of *H. armigera*.

Key words: biological control, egg parasitoids, mass rearing, parasitism, fecundity, longevity, maternal age, sex ratio.

Introduction

Egg parasitoids in the genera *Trichogramma* and *Trichogrammatoidea* (Hymenoptera Trichogrammatidae) have been successfully used in biological control programs against different pests, particularly Lepidoptera (Greenberg *et al*., 1996; Adom *et al*., 2020; Karimoune *et al*., 2020; Zang *et al*., 2021). One reason is the easiness to mass rear them on factitious hosts and their high efficiency in suppressing pest population before any damage is caused (Li, 1994; Greenberg *et al*., 1996; Para, 1997; Mills, 2010; Wang *et al*., 2014; Jalali *et al*., 2016).

The ability of a parasitoid to suppress a pest population is influenced by its fecundity and by the sex ratio of its progeny (Smith, 1996). Fecundity is one of the major biological attributes that influence the ecology and population dynamics of insects (Price, 1997). Herein, fecundity is defined as the lifetime reproductive capacity of a parasitoid in terms of the total number of eggs produced (Abrahamson, 1989; Godfray, 1994; Mills and Kuhlmann, 2000).

Sex ratio in parasitoid cultures during mass rearing is one of the major problems affecting the success of biological control programmes. The majority of parasitic Hymenoptera have a haplo-diploid reproduction, where males develop from unfertilized eggs through a form of parthenogenesis known as arrhenotoky, while females develop from fertilized eggs (Godfray, 1994; Gordh *et al*., 1999; Hawkins and Cornell, 1999). Hence, female is able to determine the sex of the offspring through the regulation of sperm access to eggs, from spermatheca where it is stored after copulation (Godfray, 1994; Gordh *et al*., 1999; Hawkins and Cornell, 1999). Female age of parasitoid is one of the important factors known to influence sex allocation during parasitism (Godfray *et al*., 1991).

While bacterial endosymbionts such as *Wolbachia* is also known to induce thelytoky (parthenogenesis in which females are produced from unfertilized eggs) in parasitoids, several studies have demonstrated that even though the sex ratio of the progeny becomes more female biased, the fitness of parasitoid is negatively affected (Yang *et al*., 2008; Liu *et al*., 2018; Zhou *et al*., 2019).

Trichogrammatoidea lutea Girault (Hymenoptera Trichogrammatidae) is indigenous to southern Africa (Parson and Ullyett, 1936; Nagarkatti and Nagaraja, 1977; Sithanantham *et al*., 2001). It is a facultative gregarious polyphagous egg parasitoid of Lepidoptera pests (Kfir, 1981), including the African bollworm *Helicoverpa armigera* (Hubner) (Lepidoptera Noctuidae) (Parson and Ullyett, 1936; Jones, 1937; Kfir and Van Hamburg, 1988; Van Den Berg *et al*., 1993; Bourarach and Hawlitzky, 1989; Fry, 1989; Haile *et al*., 2000; Van Hamburg, 1981), the spotted stemborer *Chilo partellus* (Swinhoe) (Lepidoptera Crambidae) (Nagarkatti and Nagaraja, 1977; Kfir, 1990) and the codling moth *Cydia pomonella* (L.) (Lepidoptera Tortricidae) (Pettey, 1916; Wahner, 2008). Several studies assessed the suitability of *T. lutea* as a biological control agent against *H. armigera* and *C. pomonella* from the early 1900s to early 2000s (Parson and Ullyett, 1936; Jones, 1937; Kfir, 1982; Kfir and Van Hamburg, 1988; Wahner, 2008; Mawela *et al*., 2010; 2013). However, no detailed study is available on its age-related reproductive biology, and the same is true for life tables. Knowledge on the age-related reproductive biology of *T. lutea* is important both for the development of mass rearing protocol and to assessing its potential for augmentative biological programs. In this study, we determined longevity of adults, age-specific fecundity (total number of viable offspring produced by a female parasitoid per day) and realized fecundity (total number

of viable offspring produced during the lifetime of a female), daily parasitism, number of progeny per egg and sex ratio of the progeny of *T. lutea* on eggs of *H. armigera.* In addition, the life table of *T. lutea* was also constructed to estimate population dynamics by net replacement rate (R_0), generation time (T) and intrinsic rate of population increase (r_m).

Materials and methods

Insect cultures

T. lutea and *H. armigera* were obtained from cultures from the insectary of the ARC-Plant Health and Protection (ARC-PHP) at the Rietondale campus in Pretoria, South Africa (25°43'38.90S 28°14'14.23E). Cultures were maintained as described by Mawela *et al*. (2010). *T. lutea* was reared on eggs of *H. armigera*. Prior exposure to *T. lutea*, the eggs of *H. armigera* were UV-irradiated for 15 minutes with a UV light tube (TUV 30W/G30T8, Philips, Holland; 254 nm; in a fitting with a reflective aluminium backing) to limit cannibalism which is common in larvae of *H. armigera* (Kfir and Van Hamburg, 1988; Mawela *et al*., 2010).

Longevity and reproductive biology of *T. lutea*

To determine age-specific reproductive biology of *T. lutea*, newly emerged adults (less than 24 hours old) were paired (1 male and 1 female) and transferred to small glass vials (85 mm high × 10 mm diameter), one pair per vial. Thin streaks of honey were added in the vials for adult *T. lutea* to feed on. Each *T. lutea* pair was supplied daily with a batch of 20 UV-irradiated eggs (< 24 h-old) of *H. armigera* on filter paper until all parasitoids (male and female) died. This was replicated 40 times. The experiment was carried out in an incubator (Labcon™ LTGC 20, Laboratory Marketing Services CC, Roodepoort, South Africa) maintained at 25 ± 1 °C, 60 ± 2% RH and 16L:8D photoperiod. The date and time of death of each parasitoid were recorded daily. Because *T. lutea* is a facultative gregarious parasitoid, percent parasitism was determined by the number of eggs that turned black (Kfir, 1981), while fecundity was determined as the total number of viable offspring produced per female in a vial. Progeny production, i.e. age-specific fecundity, and the sex ratio in each replicate were determined daily. Average realized fecundity was estimated by dividing the total number of progeny by the number of females.

Life table

A cohort life table was constructed using the data on age-specific survivorship (l_x) of *T. lutea* female on *H. armigera* and the number of female offspring produced per female per day until death (m_x). The population growth statistics calculated include net replacement rate [$R_0 = \sum(l_x \times m_x)$], mean generation time [$T = \sum(x \times l_x \times m_x)/\sum(l_x \times m_x)$], and intrinsic rate of population increase [$r_m = \log_e R_0/T$] (Price, 1997).

Data analysis

The data on male and female longevity of *T. lutea* were analysed by using the analysis of variance (ANOVA) for unbalanced design. Where differences were significant t-probabilities of pairwise differences were computed to separate means at $P < 0.05$. Relationships between percent parasitism, fecundity, number of progeny per egg and sex ratio of progeny to age of *T. lutea* were determined using regression analyses weighted for number of females per age. Data for females older than 11 days were excluded from the analysis in order to stabilize the variance. The significance level was set at $P < 0.05$. The data were analysed using GenStat ® (Payne *et al*., 2007).

Results

T. lutea females lived significantly longer than males with a mean longevity of 8.6 and 5.6 days, respectively ($F_{1,78}$ =12.92, $P < 0.01$) (figure 1a). The observed longevity for females ranged from 1-16 days while that of males ranged from 1-14 days. *T. lutea* parasitized the eggs of *H. armigera* from the day of eclosion. Percent parasitism was highest on day 1 (34%) and decreased to 1.6% on day 14 (figure 1b). No eggs were parasitized by *T. lutea* after 14 days.

The highest mean daily fecundity per female was 14 on the first day and decreased significantly to less than 2 with an increase in age of the females (figure 2a). The average realized fecundity of *T. lutea* was 52 offspring per female, ranging from 1-93 offspring per female. The net replacement rate (R_0) was estimated at 25.5; generation time (T) was 9.79 days and intrinsic rate of increase (r_m) was 0.33. The number of progeny per egg was highest at 2.2 on the day of eclosion, then decreased to 0.9 on day 8, and increased up to 2.0 on day 13 ($F_{13,247}$ = 18.24, $P < 0.001$) (figure 2b).

The daily sex ratio of *T. lutea* progeny was significantly female-biased from day 1 to day 3 and thereafter male-biased reaching 100% males from day 9 to day 14 (figure 2c). However, the overall percentage of male and female progeny of *T. lutea* on eggs of *H. armigera* was not significantly different, with 51% males and 49% females.

Discussion

Biological attributes of parasitoids directly influence their success as biological control agents (DeBach and Rosen, 1991; Smith, 1996; Hawkins and Cornell, 1999; Mills, 2005; Zang *et al*., 2021). Knowledge of the reproductive biology of *T. lutea* is important for the development of mass rearing systems and biological control programs (Etzel and Legner, 1999; Gordh *et al*., 1999; Kalyebi *et al*., 2006; Mawela *et al*., 2013). In this study, *T. lutea* longevity of males and females, as well as daily parasitism, fecundity, number of progeny per egg, and sex ratio with regard to age of female parents were determined. *T. lutea* females lived longer than males, and this is common in Hymenoptera as males are mainly necessary for mating (Godfray, 1994). Our results on longevity of *T. lutea* are in line with 9 days reported by Wahner (2008) at 25 °C and also 7.6 and 8 days at 22 and 15 to 18.5 °C, respectively reported by Jones (1937). The longevity of *Trichogramma pretiosum* Riley (Hymenoptera

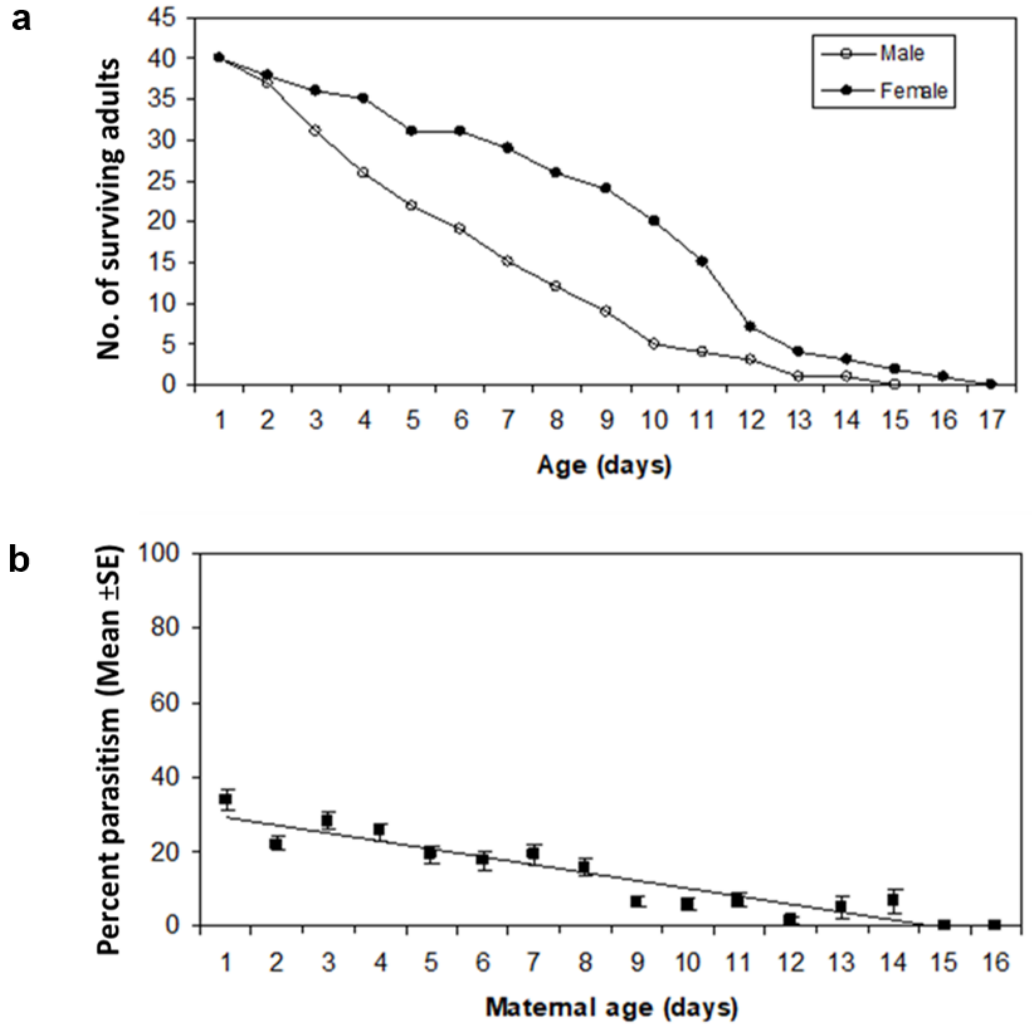

Figure 1. (a) Survival of males and females *T. lutea*. **(b)** Relationship between percentage parasitism and maternal age of *T. lutea* parasitizing eggs of *H. armigera* ($y = 33.18 - 2.46x$, $R^2_a = 0.85$, $P < 0.001$).

Trichogrammatidae) females of 8.5 days at 28 °C reported by Navarrese and Rodolfo (1997) and also that of *Trichogrammatoidea bactrae* Nagaraja (Hymenoptera Trichogrammatidae) with 7.9 days reported by Perera *et al.* (2015) at 28 °C was also similar to that of *T. lutea* female in the present study.

T. lutea did not have a pre-oviposition period since reproduction commenced on the day of eclosion. The reproductive period of *T. lutea* lasted for 14 days with no eggs parasitized from day 15 onwards. Most *Trichogramma* species are known to be pro-ovigenic (Hawkins and Cornell, 1999). Jervis *et al*. (2001) reported that the mean lifespan of synovigenic species (26 days) is greater than that of pro-ovigenic ones (9 days), which is slightly similar to the 8.6 days for *T. lutea* female. Although 20 eggs were presented to *T. lutea* daily, 100% parasitism was not achieved even on the day of eclosion. This suggests that *T. lutea* did not emerge with a full egg complement, but rather continued to mature eggs with age. Such parasitoids are referred to as weakly synovigenic (Jervis *et al*., 2001).

Daily parasitism and fecundity are not the same in the present study because *T. lutea* is a facultative gregarious parasitoid (Kfir, 1981). Nonetheless, daily parasitism and fecundity followed the same pattern, and were highest on the day of eclosion, then decreased progressively with the age of the female. The levels of parasitism in this study are similar to those reported by Garcia *et al*. (2001) for *Trichogramma cordubensis* Vargas et Cabello (Hymenoptera Trichogrammatidae) and Perera *et al*. (2015) for *T. bactrae*, where the total number of parasitized eggs decreased with the age of the female parasitoids. Similar trends were reported on *Trichogramma brassicae* (Bezdenko), *T. pretiosum* and *T. carverae* Oatman et Pinto (Steidle *et al*., 2001). However, the lifetime fecundity of the three *Trichogramma* species as reported by Steidle *et al*. (2001) (36.4, 22.8 and 9.6, respectively) was lower than that of *T. lutea* (52) in this study and that of *T. bactrae* (55) reported by Perera *et al*. (2015).

Wahner (2008) found a net replacement rate (R_0) and intrinsic rate of population increase (r_m) of *T. lutea* of 11.92 and 0.26, respectively, on *C. pomonella* at 25 °C, and both were lower compared to 25.5 and 0.33, respectively, reported in the present study at the same temperature. However, the mean generation time (T) of 9.4 days reported by Wahner (2008) was similar to that observed

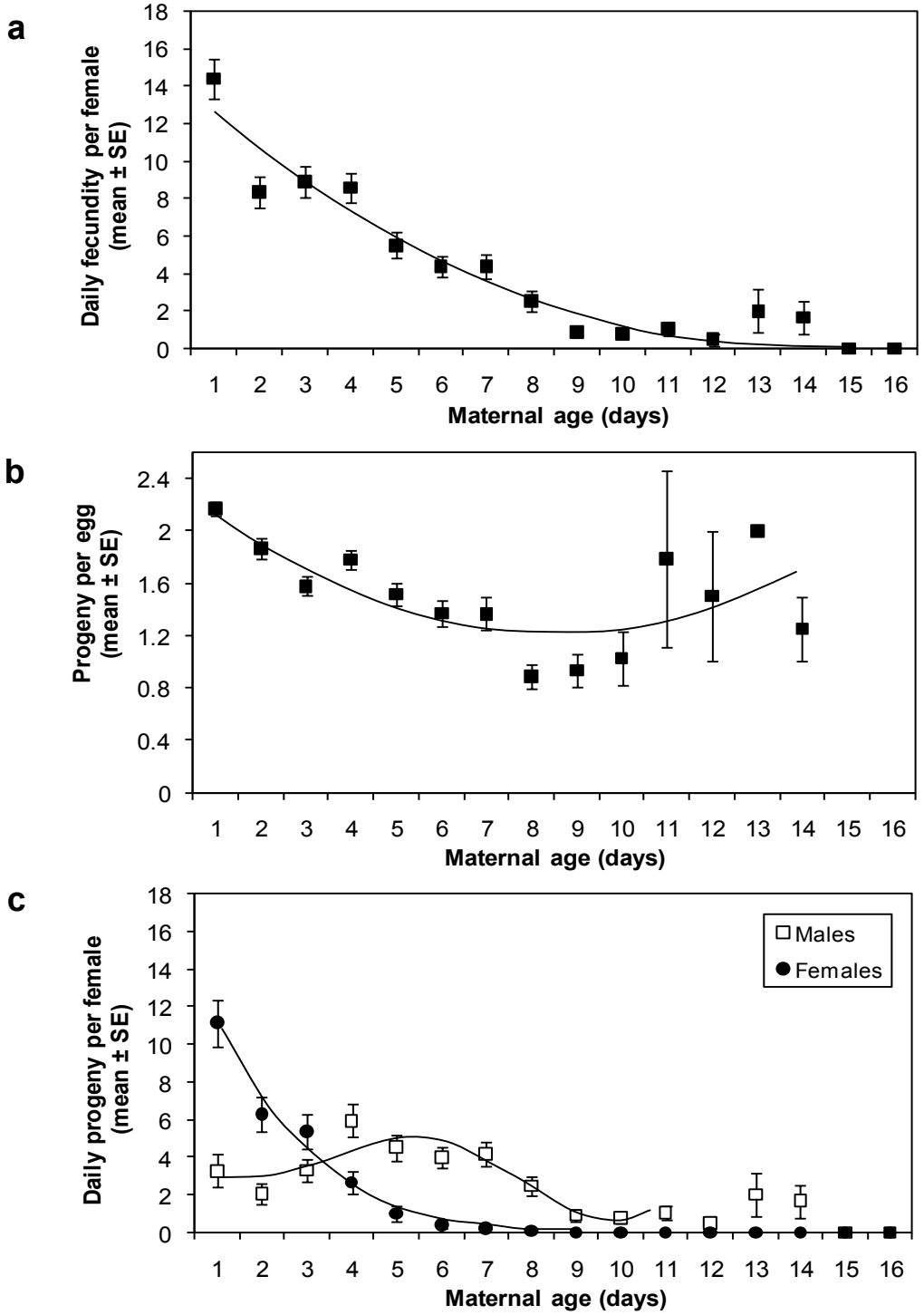

Figure 2. Relationships between maternal age of *T. lutea* and **(a)** daily fecundity per female ($y = -1.37 + 17.59 \times e^{-0.183x}$, $R^2_a = 0.92$, $P < 0.001$), **(b)** number of progeny per egg of *H. armigera* ($y = 2.410 - 0.2717 \times x + 0.01525 \times x^2$, $R^2_a = 0.72.6$, $P < 0.001$) and **(c)** male and female progeny (male: $y = 5.17 - 3.62 \times x + 1.685 \times x^2 - 0.242 \times x^3 + 0.01076 \times x^4$, $R^2_a = 0.69$, $P = 0.021$; female: $y = -0.462 + 17.86 \times e^{-0.4431x}$, $R^2_a = 0.98$, $P < 0.001$).

in this study. The net replacement rates of *T.* near *lutea* from low, medium and high altitudes reported by Kalyebi *et al*. (2006) on *Corcyra cephalonica* (Stainton) (Lepidoptera Pyralidae) at 25 °C were also lower than those of *T. lutea* in this study. Amongst other factors, differences in estimates of life table parameters of *T. lutea* reported by Wahner (2008) and the present study could be a result of different host species used (Pratissoli and Para, 2000).

T. lutea females produced both male and female offspring, showing that the female parents had been successfully inseminated (Mackauer and Völkl, 2002). However, the sex ratio of the offspring changed from female-biased during the first three days to male-biased between day 4 and 8 and thereafter 100% males from day nine. Earlier studies have shown that if female parasitoids are supplied with an unlimited number of hosts in the laboratory, the

sex ratio changes and becomes increasingly male-biased due to sperm depletion (Godfray, 1994; Pérez-Lachaud and Hardy, 1998). The decrease in the daily number of offspring produced towards the end of the experiment could be due to egg depletion (Gordh *et al*., 1999). In general, the two most important limiting factors for reproduction in parasitoids are likely to be the number of mature eggs for synovigenic and the time available for pro-ovigenic (Godfray, 1994). *T. lutea* allocated more female offsprings on the first three days after eclosion. Furthermore, it was advantageous for *T. lutea* females to allocate fertilized eggs at an early age, as this will result in high number of daughters. The number of progeny emerging per parasitized egg decreased from day 1 to day 8 and thereafter increased up to day 14.

In conclusion, *T. lutea* did not undergo a pre-oviposition period, it emerged with most of its mature eggs, and had a short lifespan and reproductive period. *T. lutea* was presumed to be a weakly synovigenic, because there was no pre-oviposition period and 100% parasitism was not achieved on the day of eclosion, showing that only a proportion of eggs was matured. The results indicate a strong influence of male and female longevity together with maternal age on daily parasitism, fecundity and sex ratio. The high net replacement rate of *T. lutea* in the present study shows a good prospect for using this parasitoid as biological control agent. For efficient mass rearing of *T. lutea*, parasitoids should not be kept more than four days in cultures because the progeny becomes male-biased from the fourth day of the experiment while achieving low parasitism. Results from this study show great potential of mass rearing *T. lutea* for augmentative biological control programmes.

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