TO THE OFFICE OF GRADUATE SCHOOL AND RESEARCH

The members of the Committee approve the thesis of Arlene Aguon Pangelinan presented July 23, 1997.

Gustav Paulay, Chairperson

Charles Birkeland, Member

Barry D. Smith, Member

Adam Asquith, Member

ACCEPTED:

Joyce Marie Camacho
Acting Dean, Graduate School and Research

8/8/97
Date

AN ABSTRACT OF THE THESIS of Arlene Aguon Pangelinan for the Degree of Master of Science in Biology presented July 23, 1997

Title: Demography and Life History of the Orangeblack Hawaiian Damselfly (*Megalagrion xanthomelas*) (Selys-Longchamp, 1876) on Oahu, Hawaii.

Approved: ______________________________

Gustav Paulay, Chairperson, Thesis Committee

The only known population of *Megalagrion xanthomelas* on Oahu persists in four artificial pools and a short (100 m), fish-free tributary of the Moanalua Stream, at the Tripler Army Medical Center (TAMC). Mark-recapture methods were used to evaluate life history parameters critical to damselfly management. The observed mean of the estimated population size of *M. xanthomelas* at the TAMC was 58 individuals. Based on the number of days spent in the egg, naiad, and adult phases, the observed estimated lifespan for a damselfly is about seven months. The observed mean adult lifespan was 18 and 15 days for males and females, respectively. However, a few adults lived a maximum of more than 2 months (males – 76 days; females – 66 days). Observed mean female fecundity was estimated at 2,304 eggs, and estimated maximum fecundity was at 18,414 eggs per lifetime. *Megalagrion xanthomelas* adults can escape from local habitat disturbances and recolonize sites upon the return of suitable habitat conditions. These life history characteristics and behaviors may explain why *M. xanthomelas* has maintained a viable population in a small isolated habitat on the most urbanized island within the State of Hawaii.

DEMOGRAPHY AND LIFE HISTORY OF THE ORANGEBLACK HAWAIIAN DAMSELFLY (*MEGALAGRION XANTHOMELAS*) (SELYS-LONGCHAMP, 1876) ON OAHU, HAWAII

by

Arlene Aguon Pangelinan

A thesis submitted in partial fulfillment of the
requirements for the degree of

MASTER OF SCIENCE
IN
BIOLOGY

UNIVERSITY OF GUAM

JULY 1997

ACKNOWLEDGEMENTS

I thank the members of my thesis committee, Gustav Paulay, Chuck Birkeland, Barry Smith, and especially Adam Asquith for assisting me throughout this M.S. program. I thank the staff from the offices of the U.S. Fish and Wildlife Service Ecoregion and Pacific Islands Office, in particular, Steven E. Miller and Karen A. Evans for their valuable comments, criticisms, and assistance which helped to improve this work. I thank Barbara Maxfield, Rod Low, and Leila Gibson for technological support and assistance with my presentation material. I also thank the Bishop Museum for the use of materials on Hawaiian damselflies. I thank my parents and family for their support during my years in graduate school. I especially thank my fiancee Don J. Caserio for his patience, assistance, and emotional support throughout this project.

TABLE OF CONTENTS

PAGE

PAGE

LIST OF TABLES

PAGE

LIST OF FIGURES

PAGE

INTRODUCTION

All native Hawaiian damselflies belong to the endemic genus *Megalagrion*. These insects appear to be derived from a single colonization of continental, freshwater, narrow-winged damselflies (Coenagrionidae) and appear to be most closely related to species of *Pseudagrion* elsewhere in the Indo-Pacific (Zimmerman 1948). *Megalagrion* comprises at least 23 species and an additional 5 subspecies (Polhemus 1993).

Historically, damselflies were among the most conspicuous native Hawaiian insects. Some species inhabited water gardens in residential areas, artificial reservoirs, and watercress farms, and some were abundant in the city of Honolulu (Perkins 1913, Williams 1936). By 1948, Zimmerman (1948) noted a decline of the more common species, particularly on the island of Oahu. Gradual loss of habitats and the introduction of alien fishes and arthropods contributed to the decline of damselfly populations throughout the state. By the late 1970s, less than six populations of the Pacific Hawaiian damselfly (*Megalagrion pacificum*) could be located (Harwood 1976, Gagné 1980, Moore and Gagné 1982), and the conservation of this species was identified as a priority by the International Union for Conservation of Nature and Natural Resources (Moore 1982). A review of the status of Hawaiian damselflies in 1981 (Gagné and Howarth 1982) led to the placement of several species on the U.S. Fish and Wildlife Service's (USFWS) list of candidate species for Federal listing (49 FR 21664) in 1995. Because of the continued decline of these damselflies, particularly on the island of Oahu, intensive surveys supported by the USFWS and the State of Hawaii were initiated in 1990. The results of these surveys demonstrated that six species of Hawaiian damselflies, including the orangeblack damselfly (*Megalagrion xanthomelas* Selys-Longchamp, 1876), are now threatened with extinction (USFWS 1995).

Historically, the orangeblack damselfly was found on all of the main Hawaiian islands except Kahoolawe. The species was most common at lower elevations (below 600 m) and bred predominantly in lentic systems such as marshes, ponds, and still pools in stream channels. Today the orangeblack damselfly is extirpated on Kauai. Three populations are known on Lanai, three on Molokai, two on Maui, and breeding populations persist at numerous localities on Hawaii (USFWS 1995).

On Oahu, the orangeblack damselfly was last reported in 1935 and was believed to be extirpated from the island (Polhemus 1994b). However, in March 1994, a small population was discovered in the pools of an intermittent stream at the Tripler Army Medical Center (TAMC) (Evenhuis *et al.* 1995). This is currently the only known population on the island, as *Megalagrion xanthomelas* is extirpated from all historical localities and suitable lowland habitats throughout Oahu (Evenhuis *et al.* 1995) (Fig. 1).

This lowland species is highly susceptible to loss of habitat. Impacts from the introduction of alien fishes in streams and the physical destruction and pollution of aquatic habitats (Polhemus 1993) have severely reduced damselfly habitats on Oahu. Although the Oahu *Megalagrion xanthomelas* population faces potential impacts from urbanization and development pressures, their continued existence can probably be maintained through proper planning and implementation of conservation practices. However, data on damselfly demography and life history (*i.e.*, survivorship, adult longevity, and fecundity) are needed to develop and implement effective conservation management plans. This information, which is presently lacking for all *Megalagrion* species, is needed to guide the development of management plans for the recovery and maintenance of stable damselfly populations

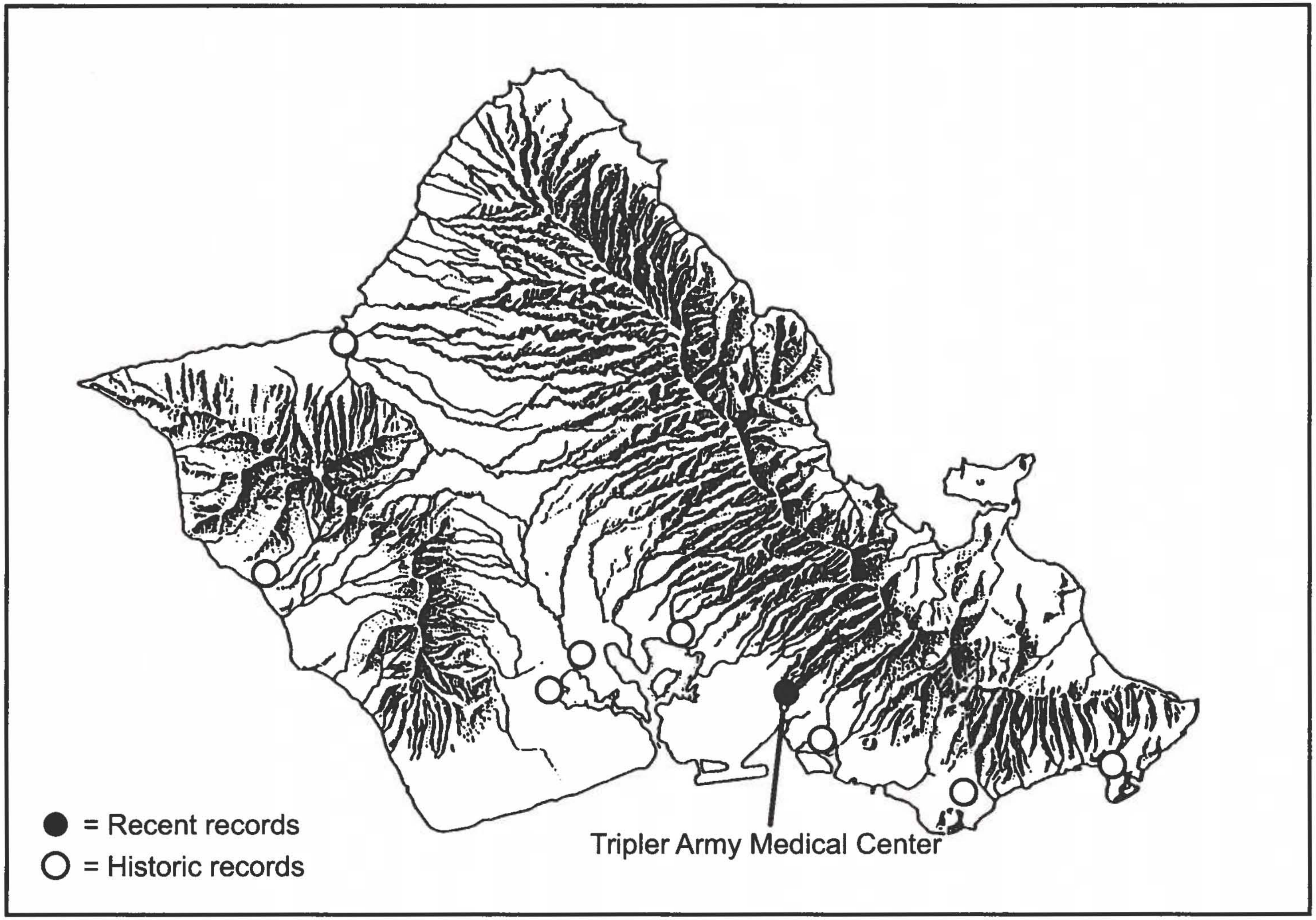

Figure 1. Map of Oahu showing locations of current and historic records for *Megalagrion xanthomelas* (Source: Evenhuis *et al*. 1995).

throughout Hawaii. To date, studies of *Megalagrion* have focused largely on taxonomy, distributional surveys evaluating habitat use, and threats contributing to their decline.

My study is the first to provide population estimates and describe life history biology of any adult *Megalagrion* species. Knowledge gained from this study can be applied to the conservation of Hawaiian damselflies and can be compared with other damselfly species throughout the state as data on those species become available. The objectives of this study are to: 1) monitor and estimate the population size, and 2) characterize life history parameters, including survivorship, adult longevity, and fecundity, of *Megalagrion xanthomelas* on Oahu. Specific questions addressed in this study are:

Question 1: What is the estimated population size of *Megalagrion xanthomelas* at the study site on Oahu?

Question 2: What is the daily survivorship of adult damselflies?

Question 3: What is the observed mean and maximum life span (longevity) of adult damselflies?

Question 4: How frequently do females lay eggs, how many eggs do they lay per oviposition event, and what is their observed mean and maximum life time fecundity?

MATERIALS AND METHODS

Study Area

Megalagrion xanthomelas occurs at two sites on the grounds of the Tripler Army Medical Center (TAMC), Oahu, Hawaii (Figs. 2 and 3). The first site includes four pools that were built in October 1995 to mitigate the potential loss of existing damselfly habitat at a tributary of the Moanalua Stream during the expansion of the TAMC. The pools are situated between a plant nursery and an existing parking lot, and they are approximately 210 m from the stream. Individual pools measure 6 m long by 1.8 m wide by 0.9 m deep. The pools are shallow depressions in the existing bench; they are lined with gunnite. The pools are directly connected to each other through a system of underground pipes. Water overflows from the highest pool into the next highest pool, and so on, until water drains into the lowest pool. The water is recirculated by a pump thro ghout each pool (Fig. 4). All four pools contain vegetation such as water lilies (*Nymphaea* spp.), water hyacinth (*Eichhornia crassipes*), and water lettuce (*Pistia stratiotes*). The entire site is surrounded by a 1.8 m-high chain-link fence that is topped with barbed wire. The perimeter of the study area is landscaped with grass to control erosion.

The second site is a tributary of the Moanalua Stream that is an intermittent stream located within a drainage gully. The tributary travels a distance of ca. 100 m on the grounds of the TAMC; it was the original site where the breeding population of *Megalagrion xanthomelas* was discovered in March 1994 (Polhemus 1994, Evenhuis *et al.* 1995). The stream is situated on the lower slopes of the leeward side of the Koolau Mountains, just

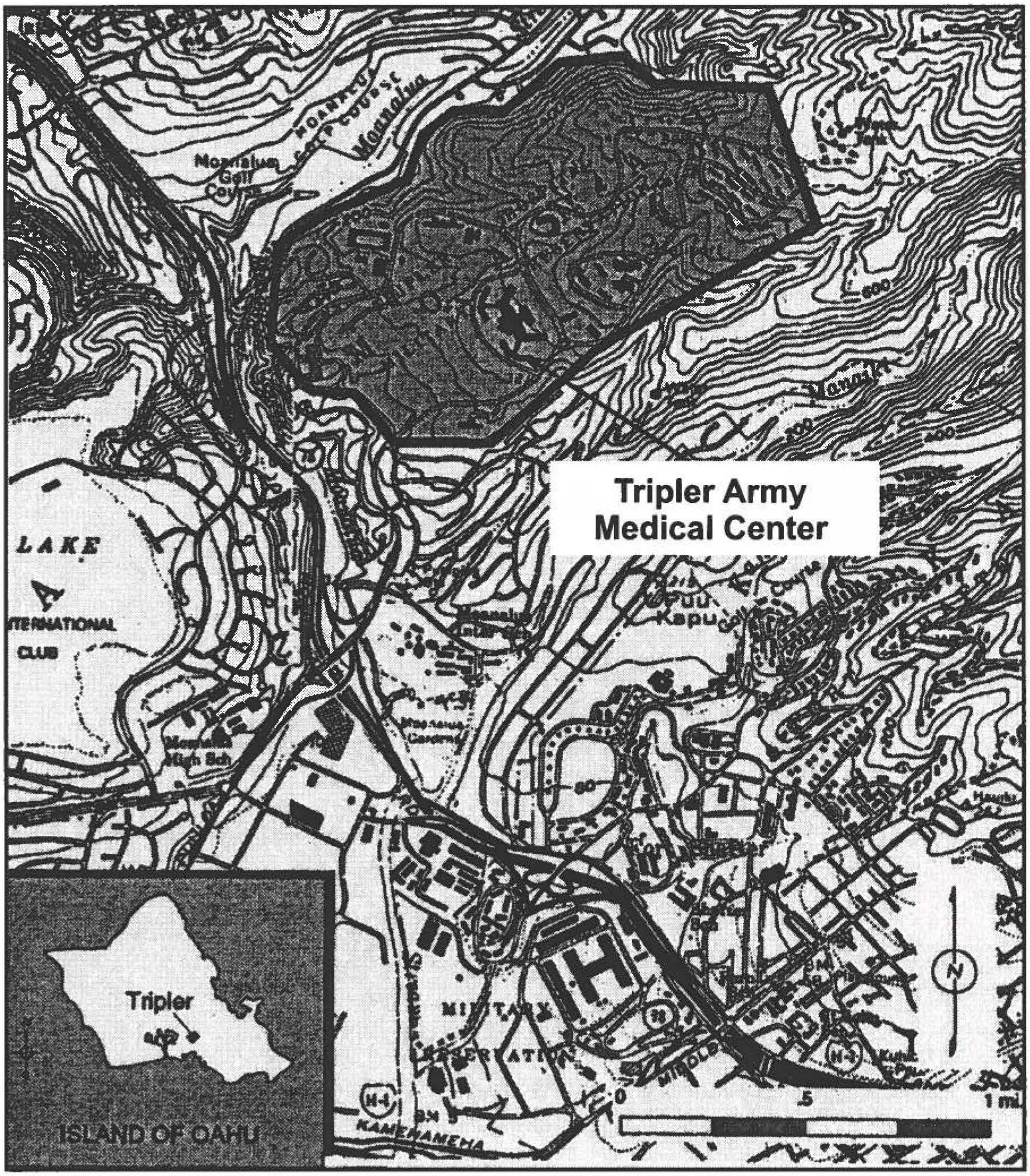

Figure 2. Location map of Tripler Army Medical Center, Oahu, Hawaii.

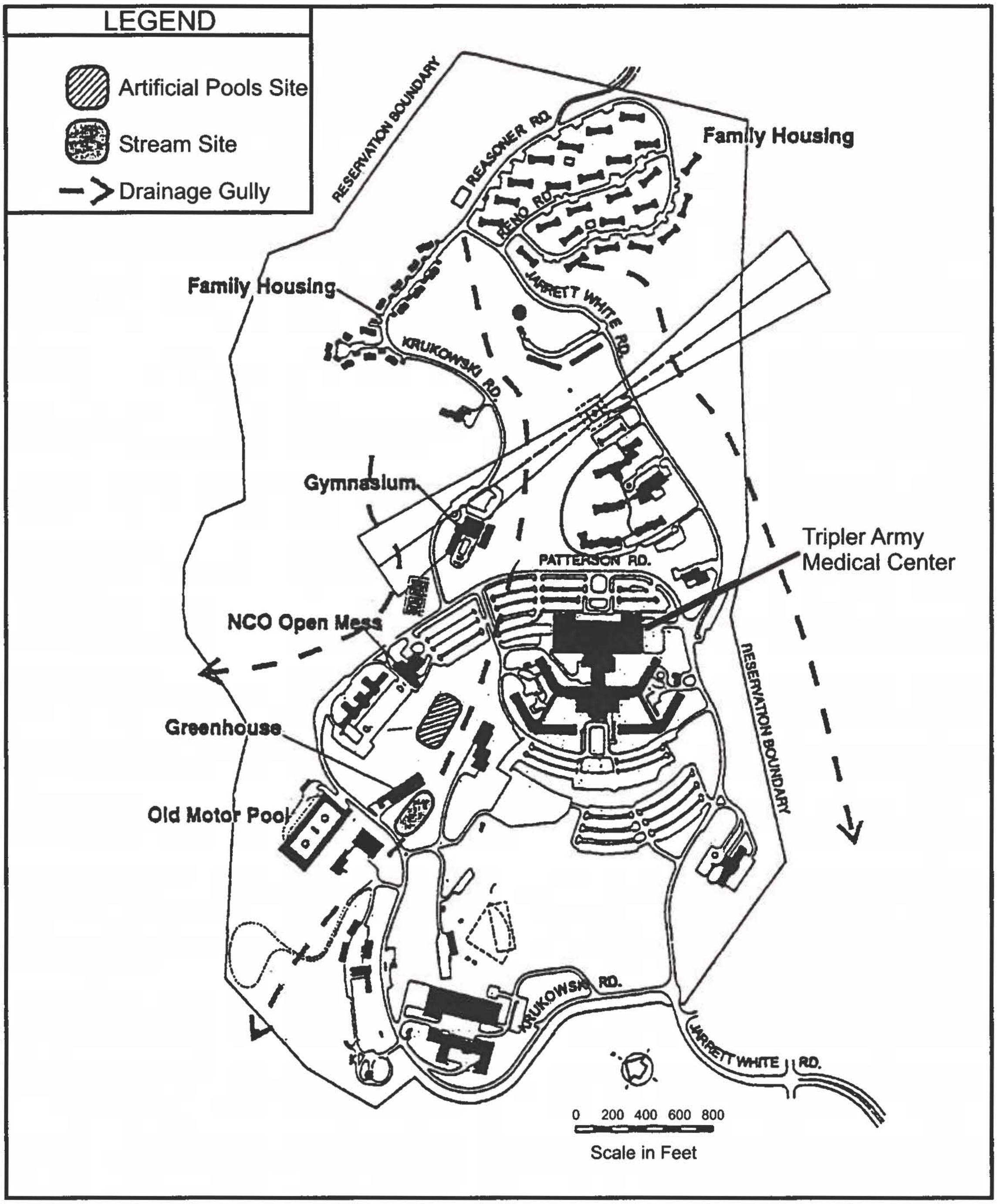

Figure 3. Study area at Tripler Army Medical Center.

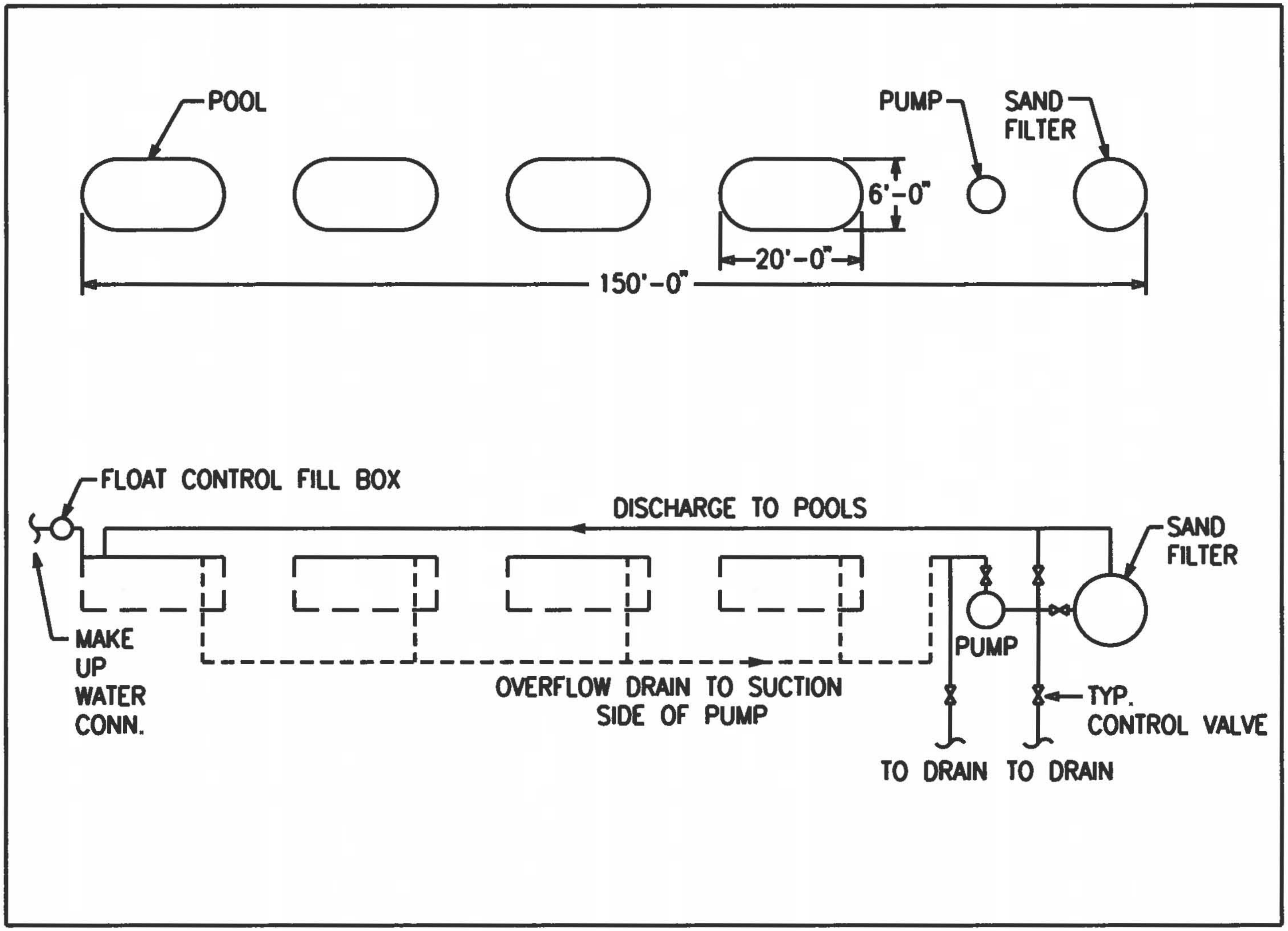

Figure 4. Artificial pool site at Tripler Army Medical Center.

south of the plant nursery and above Krukowski Road. The damselflies inhabit those areas of the drainage gully with a bedrock substrate capable of retaining water during periods of little or no flow (Evenhuis *et al.* 1995).

Study Period

The study period spanned 319 days from February 9, 1996, to December 25, 1996. Monitoring was initiated at the pools to gain information on the newly established damselfly colony. Resident damselflies at the pools were established through translocation of eggs, naiads, and adult damselflies from the stream in October 1995. Monitoring at the stream site was not originally conceived to be a part of this study.

During construction at TAMC, stream flow was disrupted. By November 2, 1995, the stream was dry, and adult damselflies had disappeared. Stream monitoring was initiated on July 30, 1996, after water flow and damselflies were observed at the site. Simultaneous (same-day) monitoring at the pools and stream were carried out from July 30, 1996 until the end of the study period. Therefore, the study period includes eleven months of pool data and five months of stream data.

Marking Technique

During each site visit to the pools and stream, I captured all unmarked individuals with an insect net and marked numbers on the right forewing with black, indelible ink. After the sex and number of each individual were recorded, damselflies were released.

Marking Effects

I tested for immediate, adverse effects of marking by holding 50 unmarked (control) and 50 newly marked (treatment) individuals in cages at each study site for 24 hours after capture. At the pools, one to three individuals were held in a 1 m x 1 m x 1 m cage; at the stream, one to five individuals were held in three separate 0.45 m x 0.45 m x 0.45 m cages. After 24 hours, those individuals that flew away were considered to be unaffected by marking.

Translocation of Damselflies

In August 1996, 60 males and 26 females were translocated from the stream into the pools to test for adult site fidelity and possible migration between sites. Surviving damselflies were included in the population estimate analysis in the study.

Sampling Methods

Study sites were sampled three times per week, weather permitting, throughout the study period. Damselflies were censused during 30-min observation periods at each of the four pools. The stream was divided into four segments based on the changes in stream elevation, and damselflies were observed during 20-min periods in each segment. I recorded the presence and activity of all marked damselflies observed, including duration of mating and egg-laying activities. Weather conditions and the time of day were also recorded.

Initial observations on damselfly activity (*i.e.*, presence at the waterbody to engage in mating or oviposition) during sunny and rainy weather indicated that it is more prevalent on sunny days and reduced or absent on overcast or rainy days (Fig. 5). Therefore, no sampling was conducted if overcast skies or heavy rains occurred on the scheduled sampling day (July 1 – 8 and November 13 – 20). For these periods, sampling was conducted on the following sunny days.

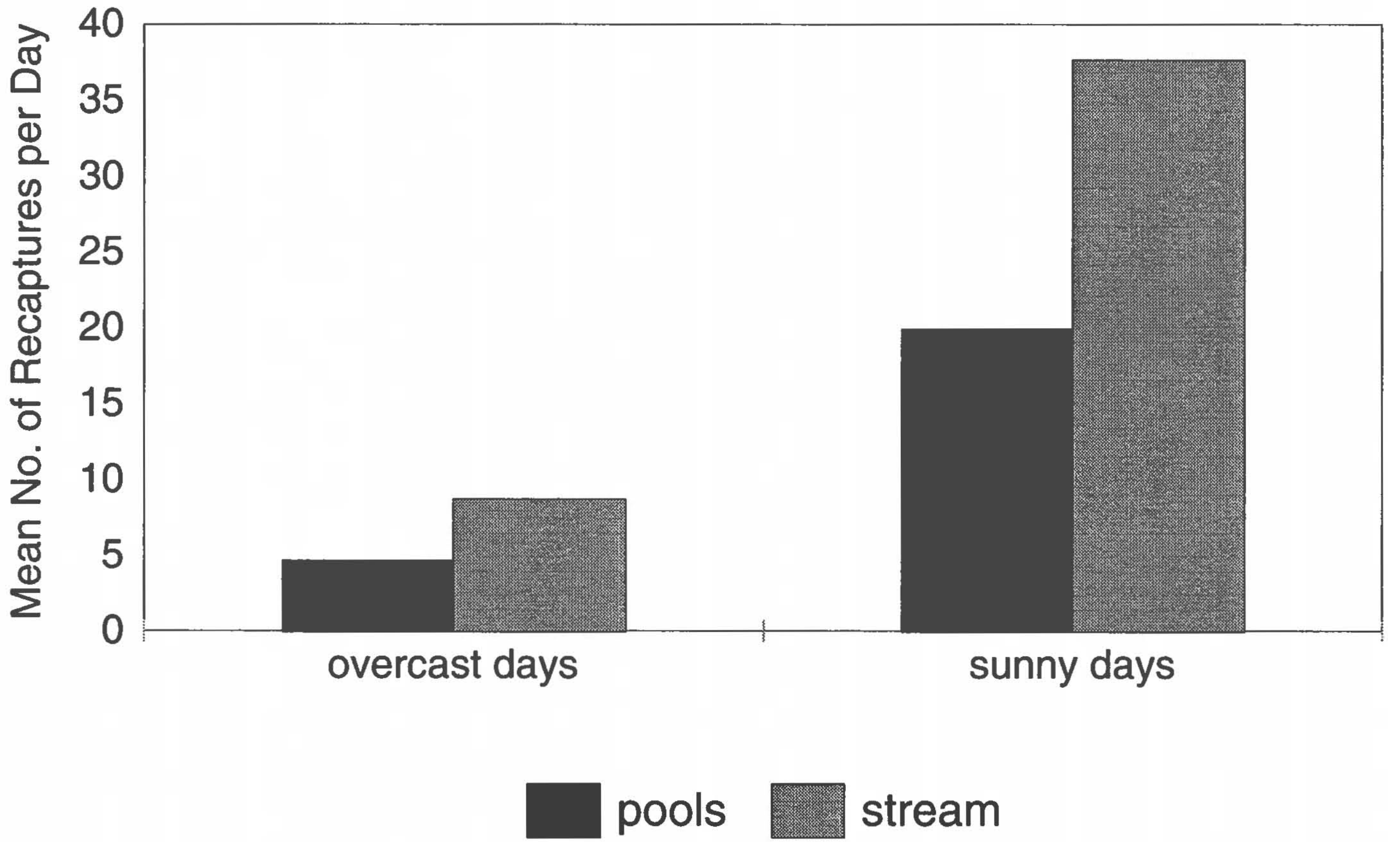

Figure 5. Effects of weather on damselfly activity.

Mark-Recapture Models

The population size and daily survival rates for *Megalagrion xanthomelas* were calculated with the mark-recapture models of Jolly and Manly-Parr (Begon 1979). The Jolly model assumes that survivorship is independent of age, and it can achieve a good estimation of population size with a fairly low rate of recaptures. The Manly-Parr model does not assume that survivorship and age are independent. However, the Manly-Parr model requires more than 10 recaptures at each sampling period to achieve a reasonable level of confidence in the population estimate.

Although preliminary calculations of the population estimates from both models were similar, the low number of recaptures, especially from the pool site, failed to satisfy the recapture criteria (> 10 at each sampling) for the Manly-Parr model. Therefore, only the Jolly model was used. The Jolly mark-recapture model (Begon 1979) calculates the following parameters:

Estimated Population Size

$$\hat{N}_i = \frac{\hat{M}_i (n_i + 1)}{(m_i + 1)}$$

Marks at Risk

$$\hat{M}_i = m_i + \frac{z_i (r_i)}{y_i}$$

Daily Survivorship

$$\hat{\Phi}_i = \frac{\hat{M}_{i+1}}{\hat{M}_i - m_i + r_i}$$

m_i the number of marked individuals caught on day *i*
n_i the number of individuals caught on day *i*
r_i the number of marked individuals released on day *i*, including those recaptured
y_i the number of individuals marked and released on day *i* and caught again subsequently
z_i the number of individuals not seen on day *i* but seen both before and after day *i*
$\hat{M}_i$ the estimated number of marks at risk on day *i* which represents a true subset population of the estimated population ($\hat{N}_i$)
$\hat{N}_i$ the estimated population size on day *i*
$\hat{\Phi}_i$ the estimated proportion of the day *i* population surviving until day *i*+1; or the chances of an individual in the day *i* population surviving until day *i*+1

Data Analyses

Population size estimates and survivorship of damselflies (males and females) at the pools and at the stream were calculated separately. An overall population size estimate and survivorship were also calculated for the combined sites during the last five months of 1996. The population and survivorship analyses include data only for days on which standardized monitoring was completed (N = 106). However, observations from visits on other days (N = 16) were included in the longevity analysis, because marked damselflies were observed in the population on those days. The translocated damselflies were not included in the population estimate on the day of movement, but they were included in the population estimates on subsequent recaptures. I report the mean ± standard deviation (S.D.) where pertinent.

Population Size Estimates at the Stream

The first 12 visits to the stream resulted in comparable numbers of individuals observed as during subsequent visits. However, the calculated estimated population size was much higher than that calculated for subsequent visits. These greater population size estimates are likely the result of the artificially high estimated : observed population size ratios of these visits, which in turn, are the result of the low number of marked individuals at the beginning of the study. To avoid this bias, the estimated population size of only subsequent (13th – 38th) visits (N = 26) were used to calculate the population size estimate for the stream and overall population.

Daily Survivorship

Daily survivorship represents the probability that an individual survives from one day to the next. Although it is biologically impossible for survivorship to exceed 1.00, the Jolly model occasionally produces estimates of survivorship >1.00. For these cases, the best estimate was assumed to be 1.00 (Begon 1979), and I adjusted the calculated survivorship values accordingly (N = 48).

I converted each survivorship value between visits into a daily survivorship value by calculating the root of the survivorship. I used the number of days between visits as the root value (*e.g.*, daily survivorship, $\phi_{daily} = \sqrt{\phi_{visit}}$ for 2 days between visits; $\phi_{daily} = \sqrt[3]{\phi_{visit}}$ for 3 days between visits; etc.).

Adult Longevity

The post-larval lifespan of *Megalagrion xanthomelas* includes a prereproductive and a reproductive phase. The prereproductive phase is defined as the time between emergence from the naiad exuvium and the onset of sexual maturation (determined by the first return of adults to the breeding site to engage in mating). The reproductive lifespan is defined as the time between the initial time and last appearance of an adult at the breeding site (Corbet 1962).

I estimated the length of the prereproductive phase based on the capture of one female teneral that emerged from the stream. The female was allowed to harden in a holding cage for 24 hours at the pools before release. I visited the pools on the first, fourth, fifth, and sixth days after release to await reappearance of the marked female. The first two visits were of < 1 hr duration, while the last two were for 4 hr each during peak activity times, as most temperate damselflies were reported to begin the reproductive phase in 4 – 7 days (Parr 1973, Fincke 1982, Hafernik and Garrison 1986).

I calculated the observed mean length of the reproductive phase of females and males based on the interval between the first and last appearance of marked damselflies in my study. The observed mean reproductive life span is less than the actual mean lifespan because damselflies lived for an unknown amount of time before their first, and past their last, known recapture event. The observed mean lifespan provides a minimum value for the longevity of this species. I summed results from the female prereproductive and reproductive phases to obtain an overall female post-larval lifespan. I did not obtain male prereproductive estimates during this study and only estimated the duration of the reproductive phase for males.

Fecundity

Fecundity was estimated as the product of the number of eggs laid per oviposition event and the number of oviposition events that a female may engage in during her lifetime.

The number of eggs laid per oviposition event was determined from: 1) direct counts of eggs laid within lily pad leaves at the pools, and 2) direct counts of mature eggs from dissection of females. Usually, an undisturbed, ovipositing female will insert all her mature eggs in a distinct, continuous, zig-zag pattern within the vegetation. They appear as amber-brown oviposition scars within 24 hours after laying.

Six females captured after copulation and prior to oviposition were dissected by Dr. Adam Asquith to count mature eggs held. Mature eggs were distinguished from immature eggs by their larger size (0.7 – 0.1 mm), yellow color, and fat, banana-like shape.

To determine the observed maximum number of lifetime oviposition events, I calculated the shortest time interval observed between oviposition events by any female. Then I divided the observed maximum female lifespan by the minimum time interval (days) between oviposition events to obtain the maximum number of lifetime oviposition events. Calculation of the observed mean number of oviposition events was made similarly, except observed mean female longevity was used; as with the observed mean female longevity, this is an underestimate of the actual mean fecundity of the species.

RESULTS

During the 319-day study period, 749 damselflies were captured and marked. Fifty-nine percent of the total marked individuals were recaptured. Males (74%) were three times more likely to be recaptured than females (24%) (Table 1). Of the 100 damselflies caged for 24 hours, only two marked males died during the observation period. The death of one male may have been attributed to exposure to adverse weather and temperature conditions, as heavy rain and wind conditions occurred during the holding period. The deaths of so few individuals from the holding cage experiment indicated that any adverse effects from marking was not significantly different between marked and unmarked damselflies (binomial, p = 0.25; *ns*).

Table 1. Number of marked and recaptured damselflies.

Site	Sex	Marked	Recaptured	% Recaptured
Pool	♂	141	113	81
	♀	101	33	33
Stream	♂	389	277	71
	♀	118	19	16
Total	♂	530	390	74
	♀	219	52	24
Combined Total		749	442	59

Megalagrion xanthomelas appears to be reproductively active year round. I observed damselflies engaging in copulation and oviposition at the pools and stream throughout the study period.

Dispersal Between Sites

Less than 2 % (8 of 442) of the recaptured damselflies were observed to move between the two study sites. Three males marked at the stream moved to the pools and remained there, and three males marked at the pools moved to the stream and remained there. One female marked at the stream moved to the pools, and one female marked at the pools moved to the stream.

In addition to the natural dispersal events described above, 86 of the 749 damselflies marked in this study were moved from the stream for release at the pools. Twenty seven of these were recaptured, all at the pools.

Population Size Estimates

I observed 10 ± 5 (range: 0 – 24, N = 106) damselflies daily at the pools. The estimated pool population size was 14 ± 8 (range: 0 – 41) (Fig. 6). I observed 26 ± 9 (range:12 – 46, N = 26) damselflies daily at the stream. The estimated stream population size was 50 ± 14 (range: 29 – 99) (Fig. 7). Overall, 31 ± 11 (range 12 – 58 , N = 26) damselflies were observed at the pools and stream. For these simultaneous visits, the overall population estimate for these two sites was 58 ± 20 damselflies (range: 30 – 94) (Fig. 8).

Daily Survivorship

Daily survivorship at the pools was 0.91 ± 0.11 (range: 0.46 – 1.00) (Fig. 9), and survivorship was 0.86 ± 0.24 (range: 0.01 – 1.00) (Fig. 10) at the stream. The overall survivorship at the two sites was 0.88 ± 0.29 (range: 0.01 – 1.00).

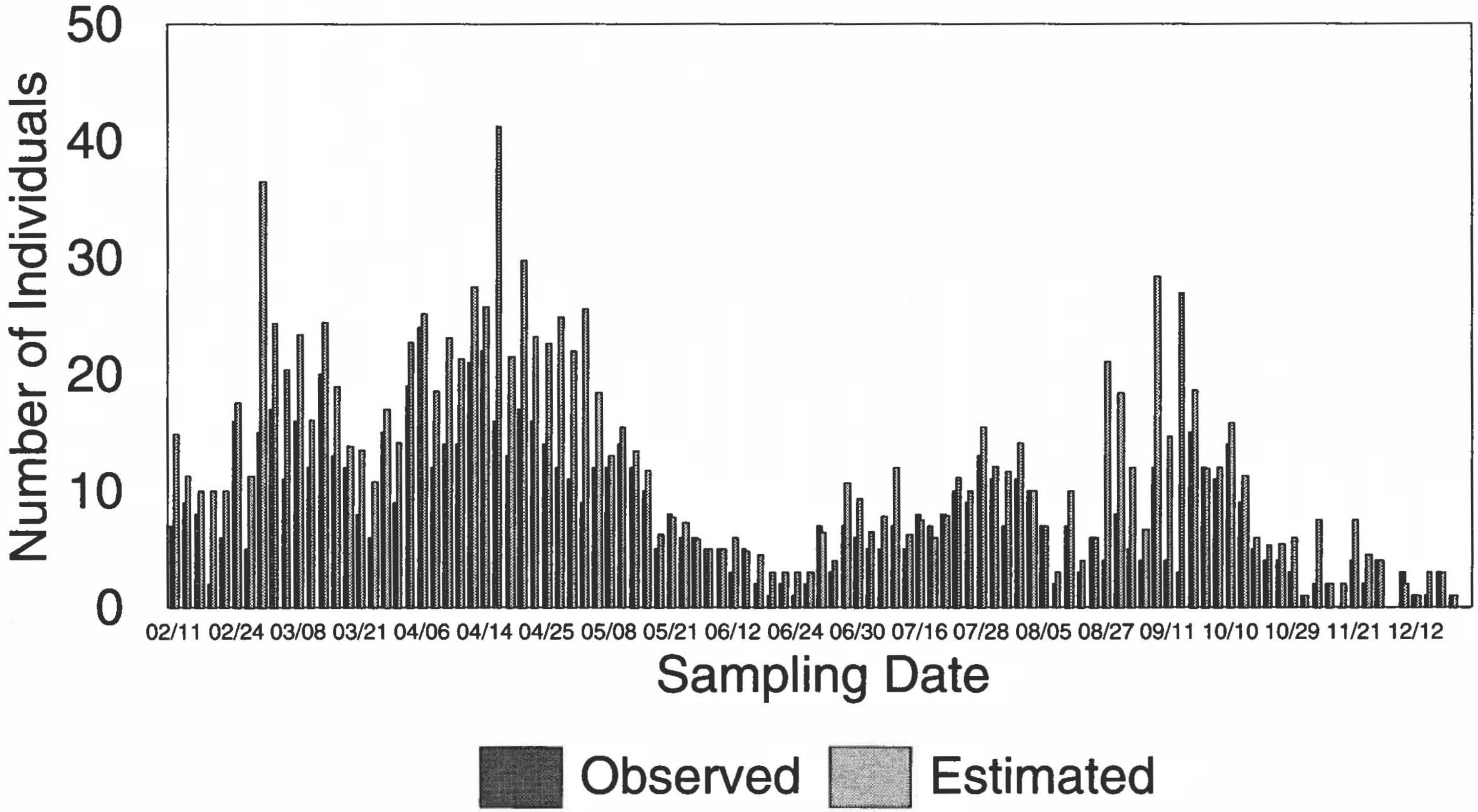

Figure 6. Observed and estimated population size at the pools.

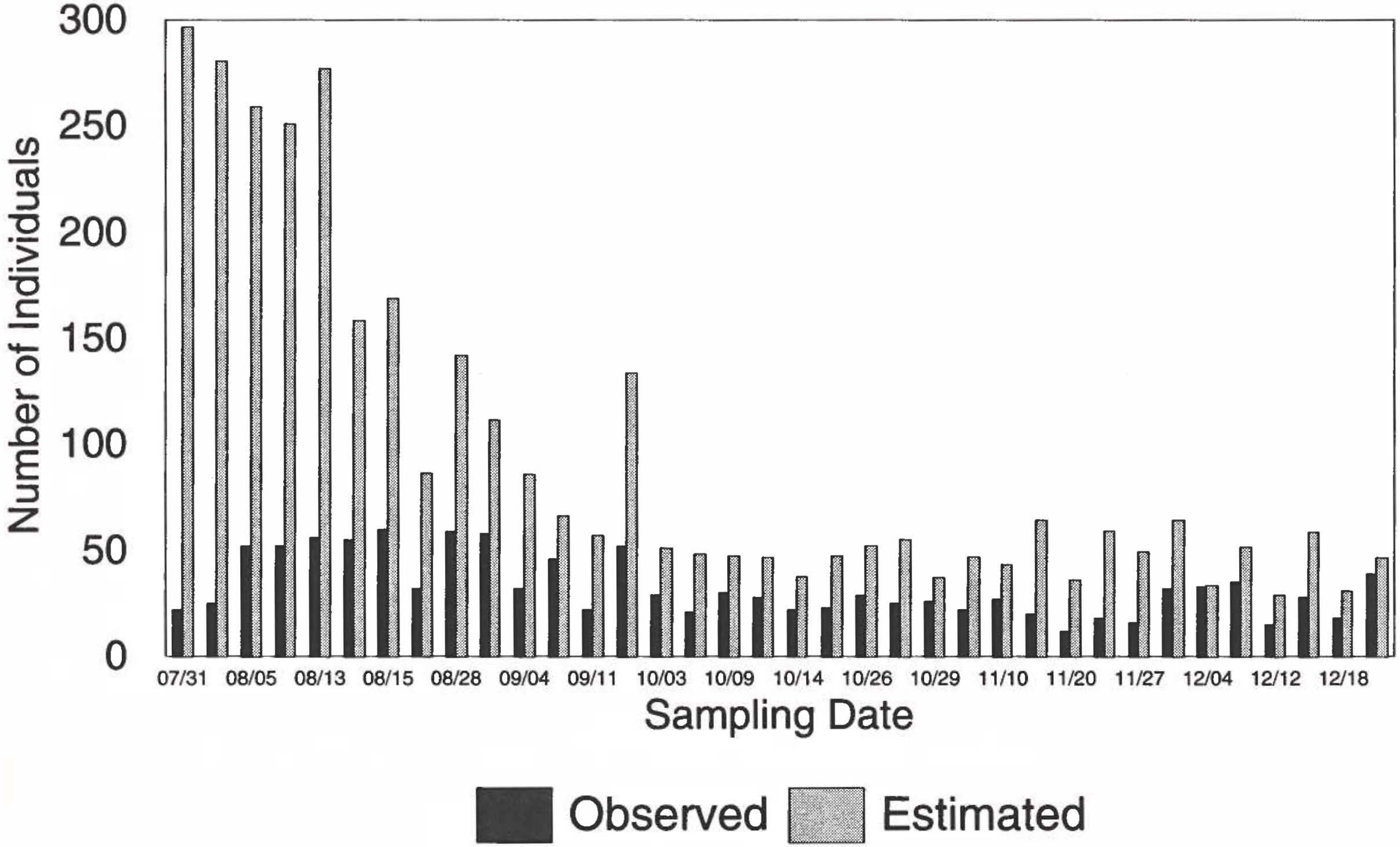

Figure 7. Observed and estimated population size at the stream. The first 12 visits were not used for calcuation of mean stream population size and overall population size estimates.

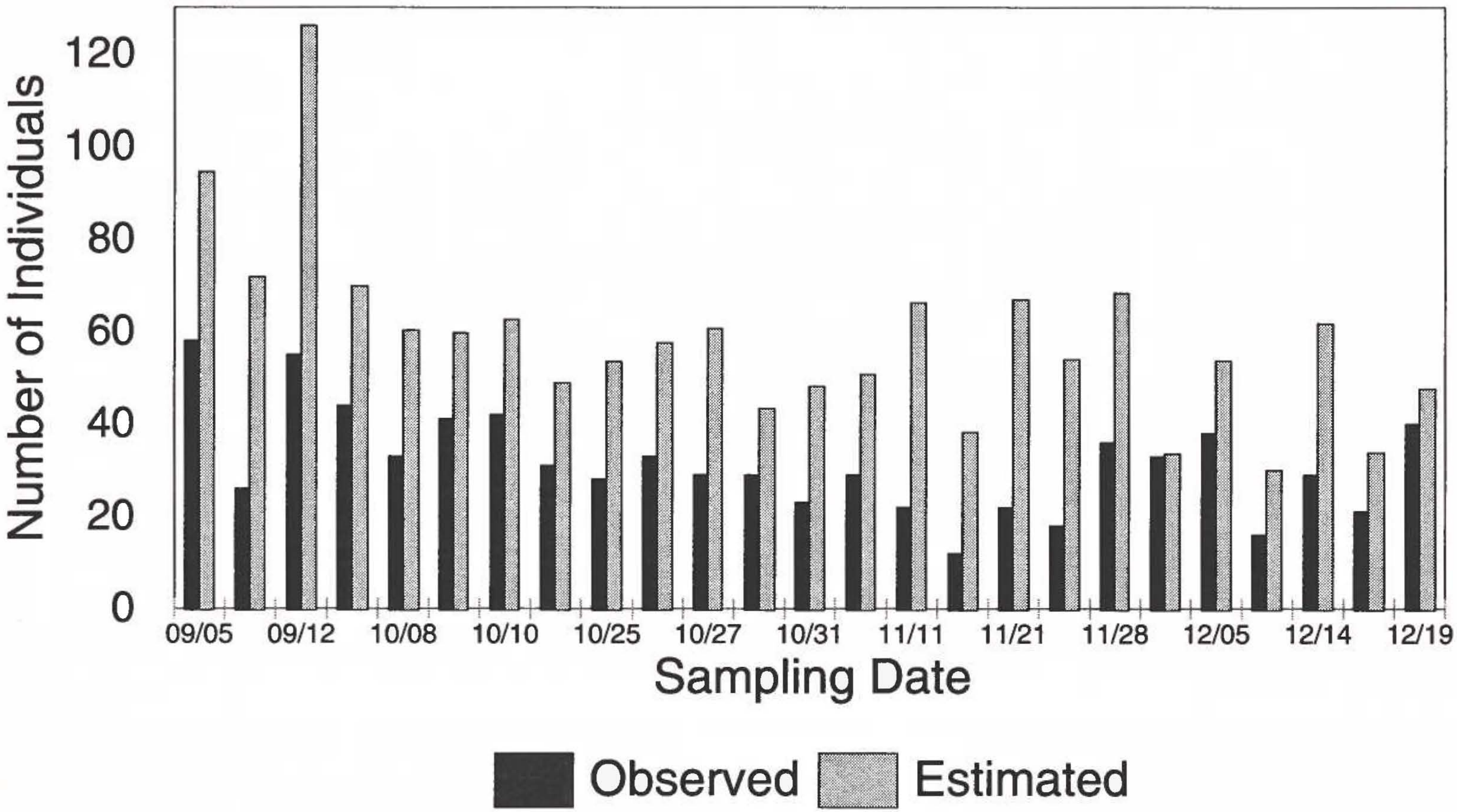

Figure 8. Observed and estimated combined population size at the pools and stream.

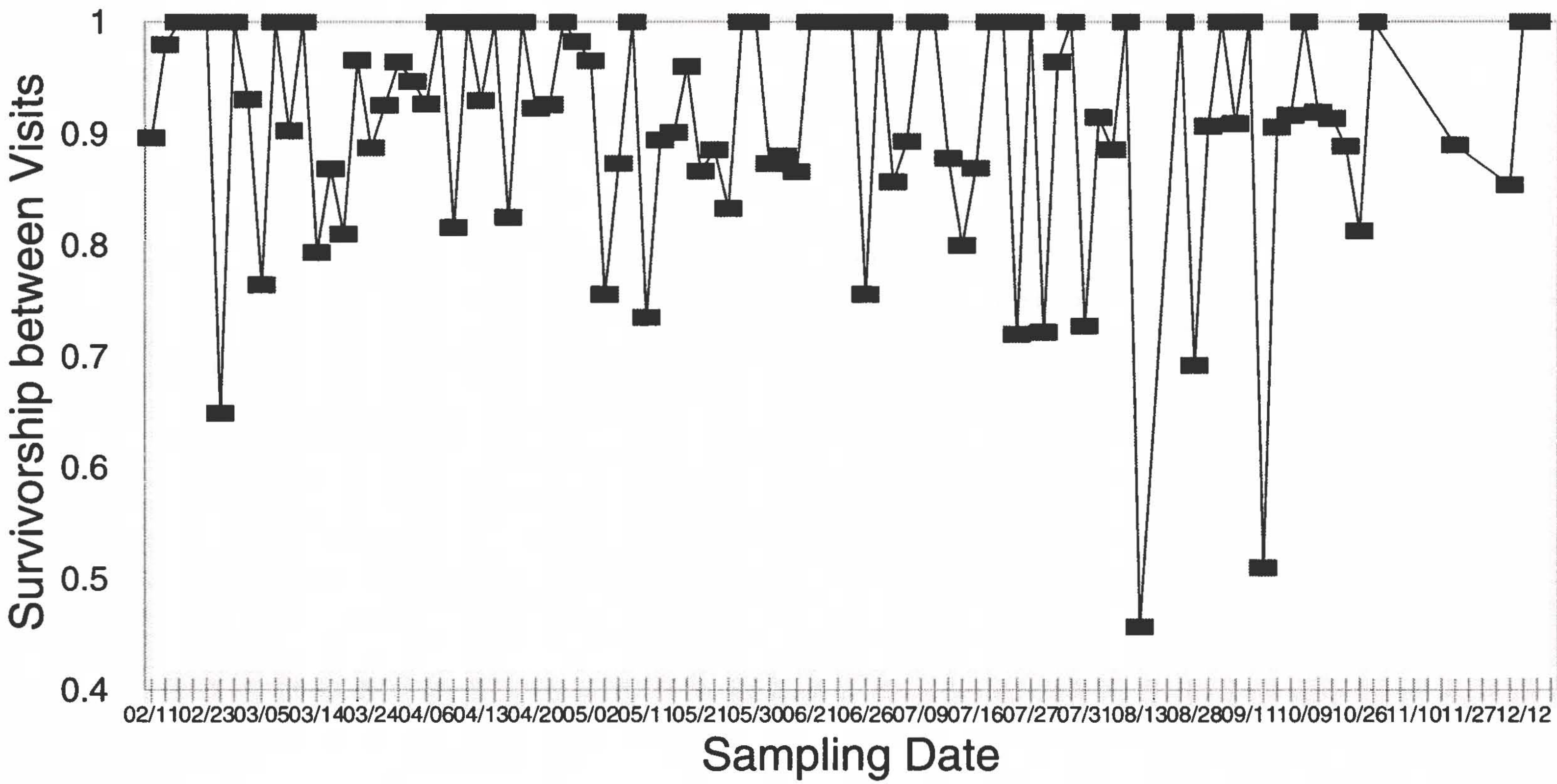

Figure 9. Daily survivorship at the pools.

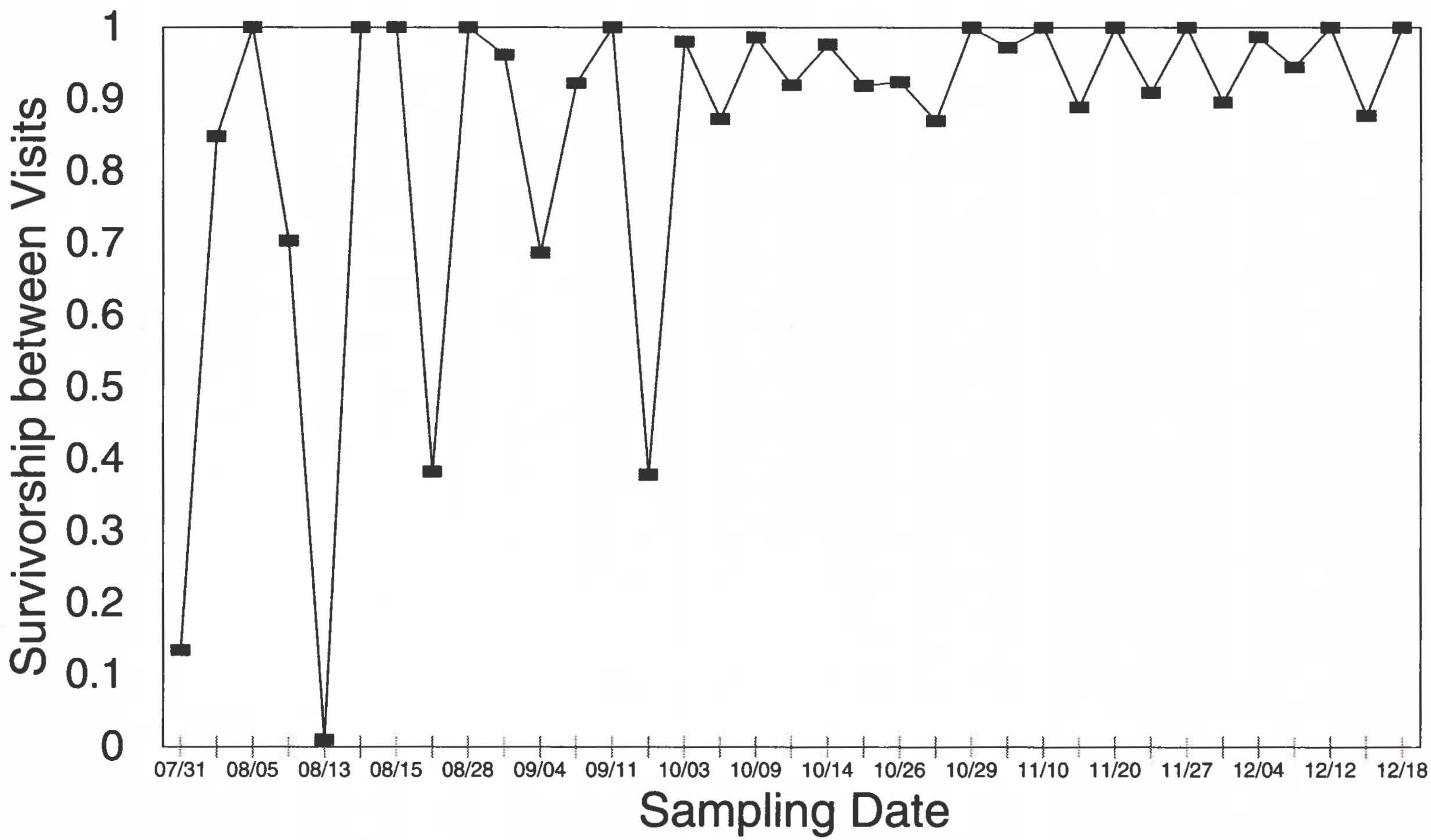

Figure 10. Daily survivorship at the stream.

Adult Longevity

Prereproductive phase

The single, immature female captured just after emergence and held for 24 hours, was first observed again at the pools six days after emergence. This is my only estimate of the duration of the prereproductive phase.

Reproductive phase

The observed mean reproductive life span of females was 15 ± 13 (range: 2 – 66, N = 52) (Fig. 11), and that of males was 18 ±15 (range: 1 – 76, N= 377) (Fig. 12). The age of almost all of the adults was unknown at the time of marking and at last recapture.

Fecundity

The number of mature eggs dissected from gravid females was 384 ± 156 (range: 170 – 558, N = 6). On two lily pads, I counted comparable numbers (208 and 515) of oviposition scars.

Direct observations of females engaged in oviposition events at the pools (N = 30) provided data on the time intervals between egg laying events. No females oviposited within 24 hours of a previous egg laying event. Oviposition was observed within 48 hours (N = 2) and 72 hours (N = 6) after egg laying. The frequency of ovipositions on the fourth and subsequent days may be combinations of the 2 – 3 day intervals between oviposition events. Therefore, the minimum interval between ovipostion is 2 days, and the average interval between egg laying events is here considered to be 2.5 days (Fig. 13).

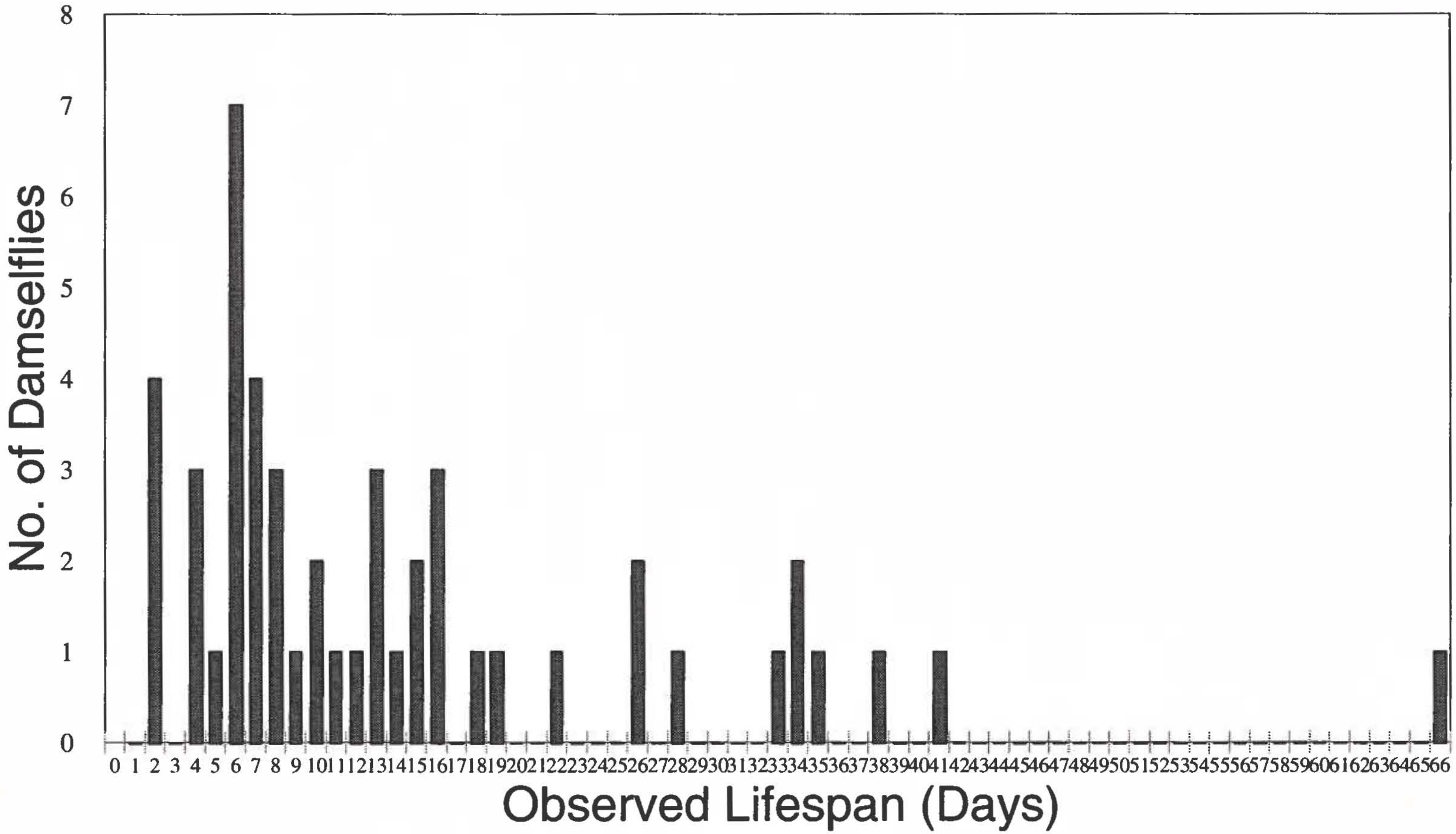

Figure 11. Observed lifespan of females.

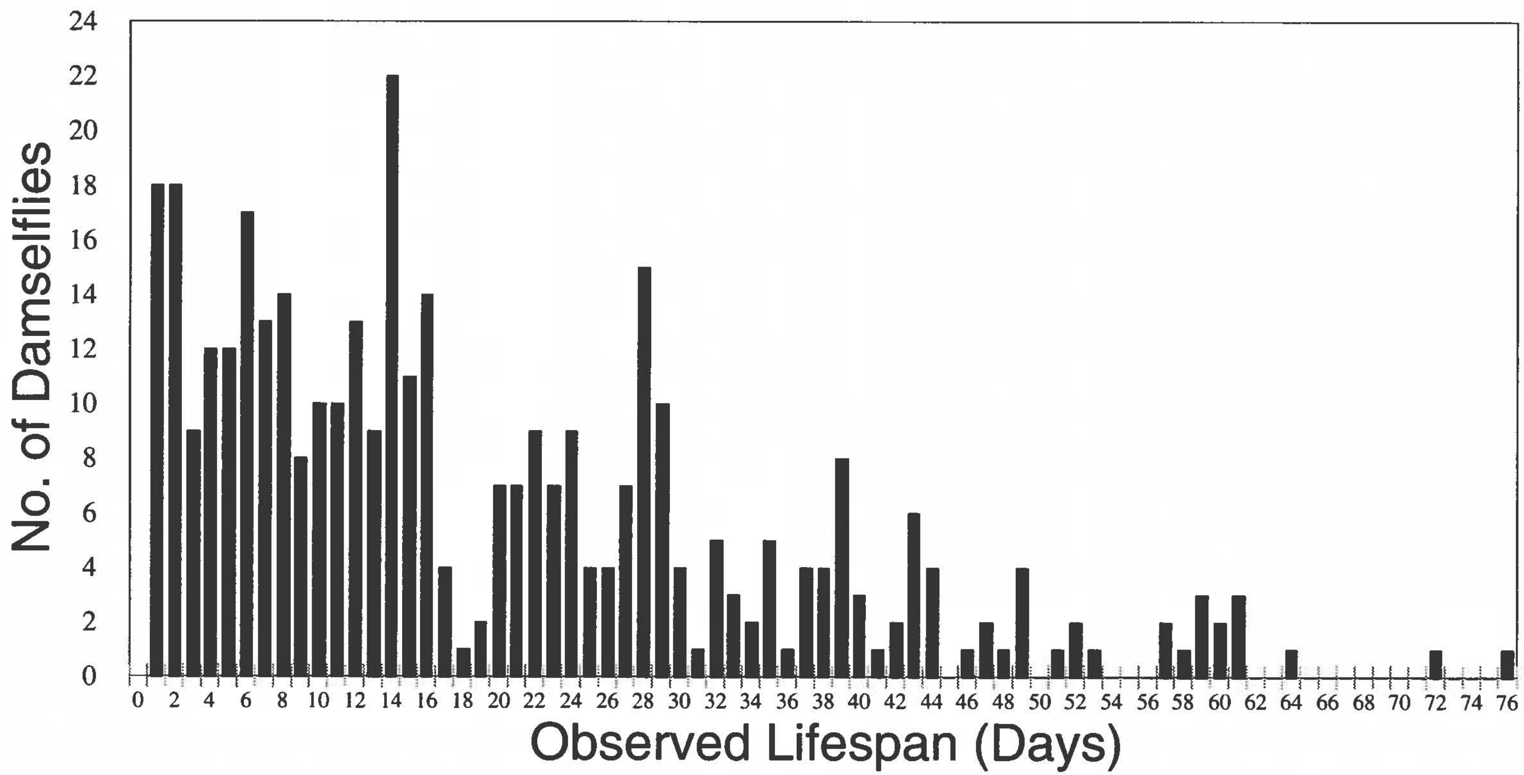

Figure 12. Observed lifespan of males.

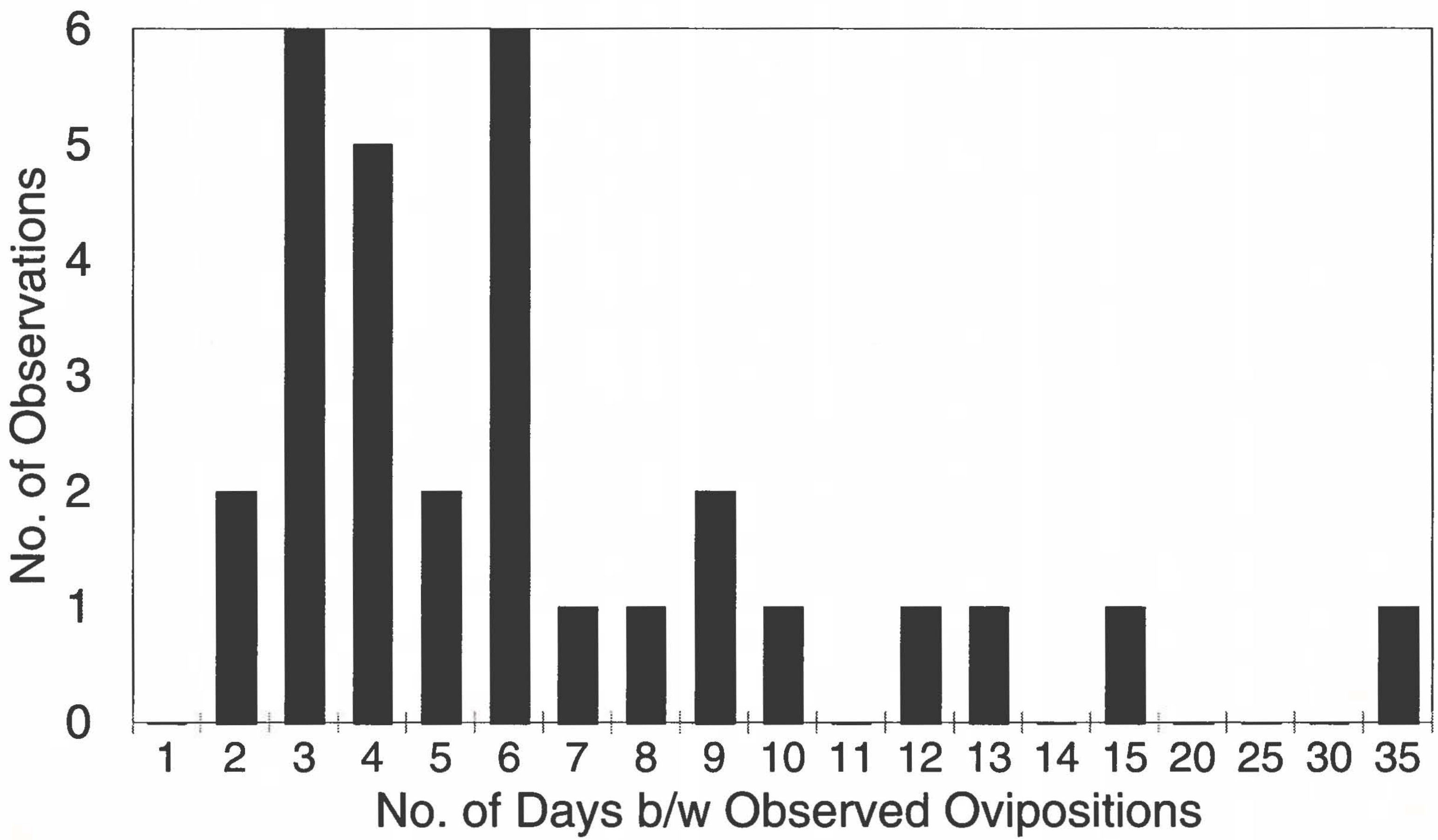

Figure 13. Frequency distribution of time interval between observed oviposition events.

Based on the longest-lived reproductive female (66 days) and a minimum two-day interval between oviposition events, a female may engage in a maximum of 33 oviposition events throughout her life time. Multiplication of the maximum number of oviposition events and the maximum number of mature eggs laid per event yields an estimate of maximum lifetime female fecundity of 18,414 eggs (Table 2).

Based on the mean observed female lifespan of 15 days and an average mean 2.5-day interval between oviposition events, a female may engage in 6 oviposition events through her lifetime, laying a mean of 384 eggs per event for an estimated mean fecundity of 2,304 eggs.

Table 2. Estimation of fecundity.

	Maximum	Mean
duration (days) of female reproductive phase	66	15
days between oviposition events	2	2.5
number of oviposition events	33	6
eggs laid per oviposition event	558	384
Life time Female Fecundity	18,414	2,304

DISCUSSION

The isolated nature of the *Megalagrion xanthomelas* population on Oahu (Evenhuis *et al.* 1995) resembles other damselfly populations that are scattered along coastal wetlands on the islands of Hawaii and Molokai (A. Asquith pers. comm.). Results of this study for the Oahu *M. xanthomelas* population may be applicable to these other isolated damselfly populations and may be useful in determining conservation actions that will enhance the survival of remaining *M. xanthomelas* populations and other rare *Megalagrion* species in the Hawaiian Islands.

Marking Effects

Megalagrion xanthomelas are relatively easy insects to work with. Their large wing size provides an adequate surface area for marking. Based on the low mortality results from the holding cage test, I concluded that marking has at most limited effects upon the survival of *M. xanthomelas*. I observed males and females engaging in copulation and oviposition activities immediately after marking. This technique probably can be safely used to assess populations of other rare *Megalagrion* throughout Hawaii.

Recaptured Damselflies

Adult male damselflies usually outnumber females at any one time at the water body (Corbet 1980). Such skewed operational sex ratios have been documented in other damselflies (Forbes 1991, Garrison and Gonzalez-Soriano 1988, Evenhuis *et al.* 1995), and accounts, in part, for the higher recaptures of males than females in my study. Behavioral differences probably account for the skewed sex ratio at the breeding site. Generally, males return daily to the water body to engage in mating, while females spend most of their time away in nearby vegetation. Females return less frequently to the water body (Hafernik and Garrison 1986) and probably spend less time when they are there to mate and lay eggs. Based on my observations, females return to the water body for oviposition at a minimum of 2 -day intervals. Recapture of females is also difficult because they are more cryptic than males (Garrison and Hafernik 1981).

Dispersal Between Sites

My observations indicate high site fidelity and low (< 2 %) damselfly dispersal between sites. This is remarkable considering that the two sites are within 210 m of each other. The repeated returns of an insect to a 'known' breeding site may be attributed to its 'homing' ability. Although no information on homing ability for *Megalagrion xanthomelas* is available, this phenomenon has been reported for other odonate species (Corbet 1962).

Site fidelity was also displayed in those damselflies that were translocated from the stream to the pools in August 1996. Therefore, translocations can be used as management tools for enhancing damselfly numbers, provided that adequate habitat conditions are available to sustain them.

Although adult damselfly mating activity is prevalent on sunny days (Fig. 5), there are occasions when no adults have been observed at the pools during a sampling visit. These absences do not necessarily demonstrate that adults are no longer resident at the site. Adults may temporarily fly away from a site in search of food or shelter (Corbet 1962). Repetitive visits to the site are needed to verify damselfly residency.

Population Size Estimate

The mean population at the pools and stream combined was estimated at 58 individuals. The significance of this estimate is unknown, as no other population size estimates for *Megalagrion xanthomelas* (or other *Megalagrion* species) are available for comparison. However, population size estimates of mature odonates from small ponds range from < 100 to > 1000 (Corbet 1980). The mean population size of *Ischnura gemina* in a small seepage area 28 m x 12 m and a linear asphalt water channel 0.3 m wide by 100 m long was 250 individuals (Garrison and Hafernik 1981). In a small beach pool of 110 m perimeter in Michigan (Fincke 1982), a mean of 121 *Enallagma hageni* males was found. In southeastern Veracruz, Mexico, in a 100-m long section of stream, a mean of 381 *Palaemnema desiderata* males was found (Garrison and Gonzales-Soriano 1988).

The Oahu population appears to be viable in the short run. However, at less than 100 individuals, the Oahu population appears probably not viable in the long run because of stochastic factors. Therefore, the establishment of new populations by translocation may ensure the integrity of the Oahu population. A subset of this population may be used as future stock for translocation to suitable habitats elsewhere on Oahu. Additional translocation studies should be conducted to determine the optimal translocation methods for enhancement of insect survival. Additional population studies on *Megalagrion xanthomelas* and other rare *Megalagrion* are needed to obtain comparative data for assessment of population size ranges for all *Megalagrion* species.

Daily Survivorship

The mean daily survivorship of *Megalagrion xanthomelas* is 0.88 and is comparable to the daily survivorship range (0.72 to 0.93) reported for other Zygoptera (Corbet 1980). *Megalagrion* adults are unique among damselflies in that they have a highly evolved behavior of 'feigning death' when caught or attacked (Moore 1983). This behavior may indicate the prevalence of predation on adults, at least in the pre-human Hawaiian ecosystem.

Adult Longevity

There are three phases in the life of Odonata after emergence: 1) prereproductive or maturation phase; 2) reproductive phase; and 3) post-reproductive phase (Corbet 1962). I only investigated the first two phases.

Ideally, longevity and survival should be measured from the emergence of tenerals. In practice, however, I had difficulty obtaining a sufficient number of tenerals that could be reared/captured at emergence, marked, and subsequently recaptured. Attempts to rear stream-caught naiads to emergence were not successful. Although one naiad was successfully reared to emergence, it did not survive the 24-hr holding period. An estimate of the length of the prereproductive phase was obtained from one female teneral captured at the stream and allowed to harden in a holding cage at the pools over a 24-hr period. This female was next observed at the pools six days later. However, it is possible that females may mature in less than six days, as my first two visits to the pools were less than one hour. Maturation time as short as 48 hr has been cited for *Calypteryx splendens* (Corbet 1962). If *Megalagrion xanthomelas* can also mature within 48 hr, then the prereproductive phase may be between 2 – 6 days.

Other female Zygoptera mature within 2 – 35 days: *Ischnura elegans* at 5.6 – 7.4 days (Fincke 1982); *Ischnura gemina* at 7 – 10 days (Hafernik and Garrison 1986); and *Megaloprepus coerulatus* at 35 days (Fincke 1992). Additional maturation periods compiled by Corbet (1962) are *Calypteryx splendens* at 2 days; *Argia moesta* at 7 – 14 days; *Pyrrhosoma nymphula* at 9 – 15 days; and *Lestes sponsa* at 16 – 30 days.

I did not obtain data on the prereproductive phase of male *Megalagrion xanthomelas*. The length of the male prereproductive phase of other Zygoptera is shorter than that of females (Corbet 1980, Banks and Thompson 1985).

Observed mean and maximum reproductive lifespans underestimate the actual longevity for the species. Maximum longevity may be close to the maximum observed lifespans for *Megalagrion xanthomelas*; 76 days for males and 66 days for females. Although my study produced a wide range of lifespans for males and females, these ranges may be the result, in part, of differences in age at first capture, lack of recapture, and natural predation pressures.

Mites such as *Limnochares americana* and *Arrenurus* spp. are known to delay development and reduce longevity of insects (Forbes and Baker 1990). There are similar phoretic mites on damselflies in Hawaii (Zimmerman 1948).

Overall Longevity

Adding the prereproductive time estimate to the age of the longest-lived female gives a maximum female longevity at 68 – 72 days. Data for overall male longevity are not available. However, the longest-lived reproductive male, at 76-days, indicates that males can live to a comparable age as females.

Tropical species often have a longer lifespan than temperate species. Temperate adult lifespans range from 24 to 50 days, while tropical lifespans range from 21 to 165 days (Table 3).

When the longevity data are coupled with the number of days spent in the egg and naiad phases, the lifespan of *Megalagrion xanthomelas* is at least seven months [egg phase – 21 days (Evenhuis *et al.* 1995); naiad phase – four months (Williams 1936, Evenhuis *et al.* 1995); and adult phase – 2.5 months (pers. obs. 1996)].

Table 3. Maximum adult lifespans of damselfly species.

Species	Days
Temperate	
Calypterix maculata (Waage 1972)	37
Calypterix virgo (Klotzli 1971, in Waage 1972)	41
Ischnura gemina (Garrison and Hafernik 1981)	♂ : 36; ♀ : 24
Ischnura elegans (Parr 1973)	♂ : 42; ♀ : 50
Tropical	
Megaloprepus coerulatus (Fincke 1992)	165
Mecistogaster ornata (Fincke 1992)	85
Mecistogaster linearis (Fincke 1992)	84
Megalagrion xanthomelas (this study)	♂ : 76 +; ♀ : 68 – 72
Palaemnema desiderata (Garrison and Gonzales-Soriano 1988)	♂ : 21; ♀ : 21

Fecundity

Because I did not monitor female oviposition events seven days per week, my observed number of oviposition events (on Tuesday to Thursday of each week) may underestimate actual oviposition frequency. In general, females are not likely to return to the water body within 24 hrs of oviposition. I observed females (N = 4) leave the pools after completion of oviposition. These same females were not observed to return to the pools to oviposit on the following day (Fig 13). Presumably, female *Megalagrion xanthomelas* oviposit all their mature eggs on the same day as mating, as documented in *Ischnura gemina* (Fincke 1982). Females probably remain in the vegetation to forage and mature new egg batches; they will not return to the water body until mature eggs are ready for oviposition. On all but two occasions (N= 219), females observed at the water body were either ovipositing or mating. The two exceptions occurred at the pools on a day when no males were present.

In other Odonata studied (*Calypteryx maculata, Chromagrion conditum,* and *Anax imperator*), about 100 – 400 eggs are laid per episode. Individual *Calypteryx maculata* can lay 525 – 750 eggs per day and 1,267 – 1,810 over a period of 4 –14 days (Corbet 1980). The mean (384) estimate of eggs laid per episode for *Megalagrion xanthomelas* are at the high end of this range.

Survival at the Stream Site

During construction activities at the TAMC, stream flow was disrupted, and by November 2, 1995, the stream was dry and adult damselflies had disappeared. Adults may have temporarily dispersed away from the site, as the existing habitat conditions were unsuitable for breeding. Adults may have persisted in the vegetation and survived long enough to recolonize the stream following the restoration of water flow. Alternatively or in part, recolonization may have been from the pools by damselflies translocated there in

October 1995. Recolonization of this small stream indicates that a temporary disruption of water flow may not necessarily cause the extinction of a stream population if aquatic conditions return prior to the death of all living adults.

Damselfly Numbers at the Pools and Stream

On average, I observed three times more damselflies per visit at the stream (28) than at the pools (10) despite the fact that available stream habitat is generally smaller than the pools. Stream habitats vary in size according to water flow, ranging from several small pockets of water in depressions along the stream gully to 1 – 2 pools of water about 1.5 m in diameter.

Another noticeable habitat difference between the pools and the stream is the greater abundance of predators at the former. The pools attract more alien dragonflies compared to the stream because alien dragonflies prefer larger open space ponds and lakes. Native damselflies prefer narrow stream corridors having an arboreal canopy and peripheral vegetation. Five dragonfly species [3 alien (*Crocothemis servilia*, *Orothemis feruginea*, and *Tramea* spp.) and 2 native species (*Pantala flavescens* and *Anax junius*)] were usually present at the pools. I rarely observed adult dragonflies at the stream, and the extent of stream vegetation made finding of dragonfly exuviae difficult. I did not find any dragonfly exuviae at the stream during this study. In contrast, 8 – 20 dragonfly exuviae were found during most sampling days at the pools. Naiads of the native dragonfly *P. flavescens* were usually visible within the algal mats at all four pools; a few *P. flavescens* naiads were found in isolated pockets of water along the stream.

The effects of predation and competition between alien and native dragonfly and damselfly naiads were not investigated in this study. However, it is likely that damselfly naiads were preyed upon by larger dragonfly naiads. Predation by alien dragonflies is expected, because four libellulid species on Oahu are known to feed on *Megalagrion* occasionally (Perkins 1913). The extent of predation by *P. flavescens* upon damselfly naiads has not been thoroughly investigated; this native predator-prey system has existed in nature for thousands of years.

Other factors affecting emergence rates that have not been investigated for *Megalagrion xanthomelas* include cannibalism or intraguild predation among damselfly naiads, as documented for the damselfly *Enallagma ebrium* (Forbes and Baker 1990). Because interodonate predation is a likely source of larval mortality in fishless ponds (Wissinger 1988), investigation of dragonfly impacts upon damselfly naiads is important for future mitigation and translocation efforts.

Additional questions are raised regarding the differences in site conditions that may have affected naiad emergence at the pools and at the stream. These questions were not investigated in this study and highlights the need future work: 1) Did the pools provide microhabitats (*i.e.*, rock size, gravel, leaves, etc) for naiads similar to that of the stream?; 2) Was the food source comparable between the pools and the stream?; 3) Did the pool habitats provide damselfly naiads shelter from the dragonfly naiads? Answers to these questions will lead to improvements to the mitigation pool system for conservation management.

Artificial Pools as Mitigation

The use of mitigation pools can promote the conservation of damselfly species in two ways. First, mitigation pools, if properly designed, monitored, and maintained, serve as temporary breeding and rearing areas for damselflies. These damselflies can eventually be relocated to natural habitats devoid of threats and contribute towards the maintenance of stable damselfly populations. If threats to damselfly existence can be managed and damselfly numbers in populations increase, it may not be necessary to list the species for protective status. Second, mitigation pools provide excellent areas for the experimental study of the life history and population dynamics of damselflies and habitat structure. Observations on damselfly behavior and ecology will help to determine future conservation actions for the species.

As part of the mitigation project, the USFWS developed criteria to assess whether the objective of providing damselfly habitat at the TAMC pools had been achieved. Success of the pools was based on the establishment of all three phases of the damselfly life cycle: egg, naiad, and adults at the pools. In October 1995, damselfly eggs, naiads, and adults from the stream were moved to the pools. Within two months, various sized naiads, newly emerging and breeding *Megalagrion xanthomelas* adults, and oviposition scars were observed (Zoll 1995). In November 1995, the pools were deemed successful based upon USFWS criteria. However, the physical conditions at the pools changed within three months after the determination of colonization success at the pools. Vegetation growth, alien toad invasions, and rapid algal growth clogging water circulation were documented through weekly monitoring. Maintenance activities, including quarterly weed control along the chain-link fence line, weekly displacement of algal growth from the edges of all four pools, daily cleaning of the pump filter, and installation of a barrier structure to prevent entry of alien toads into the pool site, were implemented in 1996. Intensive monitoring of damselfly habitat and activity and consistent pool maintenance helped preserve favorable breeding and rearing conditions for damselfly cohorts after colonization and through at least 2 damselfly generations. Establishment of damselflies at the pools could have been short lived if the population could not survive deteriorating habitat conditions at the pools

Data from this project highlight the need for long term success criteria and long range monitoring and maintenance of mitigation projects. Implementation of long range monitoring and maintenance of damselfly conditions helped achieve two successive damselfly grow outs.

CONCLUSION AND RECOMMENDATIONS

Island endemics often exhibit characteristics of extreme K-strategists, which makes them especially susceptible to extinction (Paulay, 1994). For example, the life history characteristics of the endangered Hawaiian tree snails in the genus *Achatinella* include low survivorship, slow growth, late maturity, and prolonged lifespans. These tree snails become sexually mature within 4 – 7 years and produce few young through their reproductive phase. The restricted geographic range of the Hawaiian tree snails also contributes to their extreme sensitivity to disturbance (Hadfield *et al.* 1993). Newly acquired data on the life history of adult *Megalagrion xanthomelas* contrasts those of *Achatinella*. *Megalagrion xanthomelas* appears to be similar to continental odonate taxa in their life histories. They attain sexual maturity early in their adult lifetime. This insect is also highly fecund, and its survivorship is comparable to continental Zygoptera. *Megalagrion xanthomelas* adults can escape local habitat disturbances and recolonize sites upon the return of suitable conditions. These adult life history characteristics do not explain the endangered and rare status of *M. xanthomelas*. Therefore, protection of the adult phase of *M. xanthomelas* may be less important to conservation strategies for the species than the protection of the naiad phase, which spans more than half the lifespan.

Data from mark-recapture studies can help assess the population structure and the status of Hawaiian damselflies. As the first mark recapture study for any *Megalagrion* species, my data provide baseline information for *M. xanthomelas* on Oahu and implications for other rare *Megalagrion* species. However, additional studies on *M. xanthomelas* and other *Megalagrion* species occurring in different habitats (*e.g.*, continuous streams) are needed to supplement and contribute to our overall understanding of Hawaiian damselfly ecology and conservation. Recommended studies include duplication of my population study for *M. xanthomelas* on other populations and detailed investigations on sexual selection, habitat use, host selection, predator-prey interactions, and ectoparasite-host relationships. Managers can use this knowledge to develop and implement conservation measures for Hawaiian damselflies and possibly establish viable habitat reserves for other rare *Megalagrion* populations.

With respect to the mitigation pools at the TAMC, short and long term criteria are necessary for evaluation of the overall success of mitigation projects. Recommended evaluative criteria include the initial establishment of all phases of the species' life cycle at the site and the long term maintenance of habitat conditions that will sustain a stable population for several generations. Long range monitoring and maintenance activities help achieve suitable damselfly habitat conditions and also verify the grow out of future damselfly generations.

LITERATURE CITED

Banks, M. J., and D. J. Thompson. 1987. Lifetime reproductive success of females of the damselfly *Coenagrion puella.* Journal of Animal Ecology **56**:815–832.

Begon, M. 1979. *Investigating animal abundance.* University Park Press. Baltimore, MD. 97 pages.

Corbet, P. S. 1962. *A biology of dragonflies.* Quadrangle Books, Inc. Chicago, IL. 247 pages.

Corbet P. S. 1980. Annual Review in Entomology **25**:189–217.

Cordoba-Aguilar, A. 1994. Adult survival and movement in males of the damselfly *Hetaerina cruentata* (Odonata: Calopterygidae). Florida Entomology **77** (2):256–264.

Evenhuis, N. E., D. A. Polhemus, S. Swift, K. Arakaki, and D. Preston. 1995. A study of the biology of the Orangeblack Hawaiian Damselfly (*Megalagrion xanthomelas*), with special reference to conservation of the population at Tripler Army Medical Center, Oahu, HI. Bishop Museum Technical Report 8. Bishop Museum Press, Honolulu, HI. 81 pages.

Fincke, O. M. 1982. Lifetime mating success in a natural population of the damselfly, *Enallagma hageni* (Walsh) (Odonata: Coenagrionidae). Behavioral Ecology and Sociobiology **10**:293–302.

Fincke, O. M. 1992. Behavioral ecology of the giant damselflies of Barro Colorado Island, Panama. Pages 102–113 in D. Quintero and A. Aiello, editors. Insects of Panama and Meso America. Oxford University Press, Oxford.

Forbes, M. R. L. 1991. Ectoparasites and mating success of male *Enallagma ebrium* damselflies (Odonata: Coenagrionidae). Oikos **60**:336–342.

Forbes, M. R. L., and R. L. Baker. 1991. Condition and fecundity of the damselfly, *Enallagma ebrium* (Hagen): the importance of ectoparasites. Oecologia **86**:335–341.

Gagné, W. C. 1980. Insects and myriopods of Kipahulu Valley below 2,000 feet. Pages 119–175 in C. W. Smith. Resources Base Inventory of Kipahulu Valley below 2,000 feet, Maui, Hawaii. Hawaii Cooperative National Park Resources Studies Unit, HI.

Gagné, W. C., and F. G. Howarth. 1982. Assessment of endangered and threatened status of Hawaiian arthropods. Report to U.S. Fish and Wildlife Service, in Pacific Islands Office, Honolulu, HI.

Garrison, R. W., and J. E. Hafernik. 1981. Population structure of the rare damselfly, *Ischnura gemina* (Kennedy) (Odonata: Coenagrionidae). Oecologica **48**:377–384.

Garrison, R. W., and E. Gonzales-Soriano. 1988. Population dynamics of two sibling species of neotropical damselflies *Palaemnema desiderata* Selys and *P. paulitoyaca* Calvert (Odonata: Platysticidae). Folia Entomologia Mexicana **76**:5–24.

Hadfield, M. G., S. E. Miller, and A. H. Carwile. 1993. The decimation of endemic Hawai'ian tree snails by alien predators. American Zoologist **33**:610–622.

Hafernik, J. E., Jr., and R. W. Garrison. 1986. Mating success and survival rate in a population of damselflies: results at variance with theory? American Naturalist **128**: 353–365.

Harwood, P. D. 1976. Dragonflies (Odonata) observed in Hawaii in 1973 and 1974. Proceedings of the Hawaiian Entomological Society **22**:251–253.

Moore, N. W. 1982. Conservation of Odonata - First steps towards a world strategy. Odonatologica **1**:205–211.

Moore, N. W. 1983. Reflex immobilisation in the Hawaiian endemic genus *Megalagrion* McLachlan (Zygoptera: Coenagrionidae). Odonatologica **12**:161-165.

Moore, N. W., and W. C. Gagné. 1982. *Megalagrion pacificum* (McLachlan) - A preliminary study of the conservation requirements of an endangered species. Report of the Odonate Specialist Group, International Union for the Conservation of Nature and Natural Resources No. **3**:1–5.

Parr, M. J. 1973. Ecological studies of *Ischnura elegans* (Vander Linden) (Zygoptera: Coenagrionaidae). II. Survivorship, local movements and dispersal. Odonatologica **2**:159–174.

Paulay, G. 1994. Biodiversity on oceanic islands: Its origin and extinction. American Zoologist **34**:134–144.

Perkins, R. C. L. 1913. Fauna Hawaiiensis, Volume 1. Introduction. Pages xv–ccxxvii in D. Sharp, ed.itor. Cambridge University Press, Cambridge.

Polhemus, D. A. 1993. Damsels in distress: A review of the conservation status of Hawaiian *Megalagrion* damselflies (Odonata: Coenagrionidae). Aquatic Conservation of Marine and Freshwater Ecosystems **3**:343–349.

Polhemus, D. A. 1994. A revision of the Hawaiian damselflies in the genus *Megalagrion* (Odonata: Coenagrionidae). Unpublished report to U.S. Fish and Wildlife Service, Pacific Islands Office, Honolulu, HI. 68 pages.

U.S. Fish and Wildlife Service. 1995. Hawaiian Damselfly Survey: Population Checklist of Category 1 Candidate Species. Unpublished report in U.S. Fish and Wildlife Service, Pacific Islands Office, Honolulu, HI. 84 pages.

Waage, J. K. 1972. Longevity and mobility of adult *Calypteryx maculata* (Beauvois, 1895) (Zygoptera: Calopterygidae). Odonatologica **1**:155–162.

Williams, F. X. 1936. Biological studies in Hawaiian water-loving insects. Part 1. Coleoptera or beetles. Part 2. Odonata or dragonflies. Proceedings of the Hawaiian Entomological Society **9**:235–345.

Wissinger, S. A. 1989. Comparative population ecology of dragonflies *Libellula lydia* and *Libellula luctosa.* Canadian Journal of Zoology **67**:931.

Zimmerman, E. C. 1948. Apterygota - Thysanoptera. Pages 341–380 in Insects of Hawaii, Volume 2. University of Hawaii Press, Honolulu.

Zoll, M. 1995. Orangeblack damselfly mitigation at Tripler Army Medical Center: population enhancement via artificial ponds. Unpublished report in U.S. Fish and Wildlife Service, Pacific Islands Office, Honolulu, HI. 28 pages.