A REVIEW OF TERRITORIAL AND REPRODUCTIVE BEHAVIOR IN ZYGOPTERA

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(Talk given at the Third Colloquium Dutch Dragonfly Workers, Genetics Institute, University of Utrecht; April 29, 1972)

We have worked entirely with the Zygoptera and mostly with reproductive adults. Twelve species in seven genera have been studied. I will use the coenagrionid, Argia apicalis to illustrate and then attempt a summary comparison of all 12 species. At the end, I will point out some difficulties and problems the odonate ethologists are encountering.

Most of our work was in Oklahoma at the University's Biological Station. This area is open, prairie country where during the height of the flying season it is very hot. The numerous, small, artificial pasture ponds are often very turbid and not very beautiful, but their scant vegetation made unimpeded observation and photography relatively easy.

Our equipment was: portable tape recorder, field note books, 8mm Bolex movie camera, and a 35mm Exakta still camera. We worked with individually marked males and females, applying paint in various colors to wing, thorax, or abdomen. When studying reproduction, we always attempted to follow marked pairs constantly from seizure until both members left the aquatic habitat. The constant observation of a particular pair throughout all reproductive events was difficult and often very tedious since pairs remained together for long periods, one for slightly more than three hours. Some pairs were lost at various stages so that, in addition to the complete sequences, we always accumulated many partial ones.

I. Reproduction in Argia apicalis

Argia apicalis males arrived at water earlier in the day than females, then quickly occupied a territory which they defended by activities I will describe later. The territory was a strip of shore averaging 2m long which often corresponded roughly to small irregularities of the shoreline.

Territorial behavior and the resulting rather regular spacing placed the males in advantageous positions for seizing females immediately when they arrived. For this reason, we scarcely ever saw unpaired females at the pond. Seizure was always direct without courtship, display, or signals by either member.

Quickly after seizing the female, the male transferred sperm to his second abdominal segment. The use of the term sperm translocation for this event will be discussed later. Until recently it was often assumed that this translocation occurs in unpaired males. In 1965a, we recorded the event in tandem for various zygopterans and hypothesized that it occurs in tandem throughout the Suborder. We have now observed tandem sperm translocation 87 times in 13 Zygoptera species in seven genera and have movies of the event in: *Argia plana*, *A.moesta*, *A. immunda*, *Enallagma civile*, and *Hetaerina americana*. Other workers (LOIBL, 1958; KRIEGER & KRIEGER-LOIBL, 1958; JURZITZA, 1960, 1970; HEYMER, 1966; ISHIDA, 1969) have recorded the event in tandem for: European species of *Lestes* and *Sympecma*, and for *Lestes japonicus*, *Enallagma cyathigerum*, *Ischnura pumilio*, *Platycnemis acutipennis*, *P. latipes*. Moreover, since HEYMER (1964, 1967a, 1969) and ISHIDA (1959) have now recorded sperm translocation in tandem for the anisopterans: *Epiophlebia superstes*, *Oxygastra curtisi*, *Aeshna juncea*, *Orthetrum coerulescens*, and *O. brunneum*, it seems reasonable to hypothesize that it occurs in tandem throughout the entire Order.

Copulation in *apicalis* quickly followed every observed sperm translocation. These events were always in a 1:1 ratio which suggests a translocation of sperm prior to each copulation rather than one transfer and lifetime storage. Copula occurred most often in terrestrial weeds 40cm away from water and lasted an average of 16 min. Like all other reproductive events, details of copulation varied within the same population and even within the same pair. The female held her legs in three different positions, the male rubbed the femoraltibial joints of his metathoracic legs against the female abdomen at various times, and the male pumped his abdomen at irregular intervals.

After copulation, pairs frequently shifted as the female momentarily probed almost every possible oviposition material. Because probing was so brief at any one site, it is unlikely that eggs were deposited. We designated this period, which averaged 25 min, as exploration in tandem. A pair eventually settled for effective oviposition, often at a site other than the one previously defended by the unaccompanied male. Pairs were remarkably tolerant of each other and often oviposited under very crowded conditions at what we (1965c) called communal sites. LOIBL (1958) records such great crowding in pairs of *Lestes dryas* that the females oviposited in the abdomens of other pairs. Preferred oviposition sites for *apicalis* were old boards and logs early in the season, but later adventitious willow roots became available and were utilized. During tandem oviposition, males were most often rigidly upright in the *Agrion* position of WESENBERG-LUND (1913) and BUCHHOLZ (1950). However, all males occasionally leaned forward and rested on the horizontal substrate in the *Sympecma* position. The mean time in tandem oviposition, exclusive of exploration, was 65 min. After tandem oviposition many females oviposited alone for an average of 21 min, and males seldom disturbed them even though their previous mates did not guard them. During oviposition, females never descended completely beneath the surface and never utilized vertical substrates. Thus, oviposition in the same population was both in tandem and unaccompanied, and of both the *Agrion* and *Sympecma* types. No female oviposited a second time during the same day. Most left water immediately after oviposition; those that were pursued by a male escaped primarily by rapid flight.

It is sometimes stated that one copulation fertilizes all eggs which subsequently develop. GRIEVE (1937) demonstrated that this holds for *Ischnura verticalis*, but we do not think that it holds for *apicalis* because copulation immediately preceded every oviposition. However, further work is needed to prove that actual insemination occurs with each copulation, i.e., that the observed copulation is not merely ritualistic. We can only say that all pairs constantly observed assumed the wheel position prior to each oviposition.

II. Behavior of Unpaired *Argia apicalis* males

As a preliminary to reproductive behavior we have necessarily been concerned with unpaired males, i.e., with such matters as: do they have a territory ? if so, how large ? and how is it gained and defended ? We observed a single male constantly for a 30 min interval and accumulated 17 such records. Territorial behavior of unpaired *apicalis* males included the following five activities:

1. *Wing clapping*. In this activity, right and left wings were slightly separated and then quickly brought together 1-8 times while meso- and metathoracic pairs remained close together. This action occurred with no other odonates nearby. We (1971b) considered that it probably serves as a territorial display but did not rule out the possibility of a mere comfort movement.

2. *Wing warning*. In this activity, right and left wings spread apart, meso- and metathoracic members separated, and the wings were momentarily held in this ruffled position. This action, recorded only when other individuals approached, seems fundamentally similar to the threat display which PAJUNEN (1963) records for various resting Zygoptera species.

3. *Flight toward*. The perched male flew directly toward the intruder, usually displaced him without a clash or any sexual manifestations, and then quickly returned to his perch.

4. *Flight no reason*. The perched male flew out a short distance from his perch and quickly returned. These sorties were not advances to any other odonate, were not for feeding, and were not in response to any stimulus which we could detect, hence our designation of flight no reason. Nevertheless, we (1965c, 1971b) considered that these flights function as short patrols which are important in maintaining a territory free of intruders.

5. *Circle flight*. Two males flew head to tail in a horizontal circular pattern, which seems essentially as JOHNSON (1962b) described for *Hetaerina americana*. Circle flights were rare in *apicalis* and we surmise

that they occurred only after an intruder was not readily displaced by the flight toward activity.

It seems to us that the occupant male declared that the territory was his by wing clapping and patrol flights. If an intruder advanced in spite of these declarations, more vigorous behavior occurred. This was almost entirely wing warning and flight toward, but when the chase was not quickly successful, circle flights occasionally followed. By the three latter events, the occupant male displaced 87% of the intruders and consistently maintained a territory of approximately 2m of pond margin.

III. Comparisons of Behavior

Like *Argia apicalis*, *A. plana* and *Enallagma civile* reacted aggressively to intruders, displaced 79 to 84% of them, and maintained small territories of 1m and 20cm respectively. In contrast, *Lestes unguiculatus* males often showed no aggressive reactions and abandoned their perches to 61% of the intruders. *L. unguiculatus* was markedly unsuccessful in maintaining territory.

The behavior of unpaired males of the four species (*Argia apicalis*, *A. plana*, *Enallagma civile*, *Lestes unguiculatus*) for which we have quantitative data was obviously less complex than the flight maneuvers which we observed from time to time among males of *Hetaerina americana* and among those of *Calopteryx maculata*. In *americana*, the resident male flies toward the intruder and the two then fly in a head-tail pattern of gradually increasing circles (JOHNSON, 1962b; BICK, unpub. observations). In *maculata*, the antagonists fly close to each other then hover face to face with abdominal tips elevated (JOHNSON, 1962a; BICK, unpub.). This *maculata* behavior seems similar to, but is apparently less complex than PAJUNEN's (1966) description of frontal threat in *Calopteryx virgo*.

Based primarily on the Zygoptera we have studied, it seems that at least four kinds of territorial situations occur. These are:

(1) Occupancy of a single stem with little aggressive behavior yet recorded. Examples are: *Lestes disjunctus* (BICK, 1961): *Lestes unguiculatus* (BICK & HORNUFF, 1965), *Archilestes grandis* (BICK, unpub.). We now think that more persistent observation will reveal some aggressive behavior even in the apparently very passive behavior of many species, and that entirely passive occupancy is an impossibility.

(2) Occupancy of an area, which is sometimes very small, by means of aggressive behavior not involving complex flight maneuvers. Examples are: *Argia apicalis* (BICK, 1965c); *A. plana* (BICK, 1971), *A. moesta* (BICK, unpub.); *Enallagma civile* (BICK, 1963).

(3) Occupancy of an area primarily by complex flight maneuvers as has been demonstrated by many for *Calopteryx* spp., by JOHNSON (1961, 1962b) for *Hetaerina americana*, and by HEYMER (1966) for *Platycnemis acutipennis*.

(4) A constant cruising by males who scarcely ever perch at one spot. Examples are: *Ischnura verticalis* (BICK, unpub.); *Enallagma aspersum* (BICK & HORNUFF, 1966). This situation seems to parallel the behavior described by HEYMER (1968) for certain non territorial anisopterans actively searching for females.

There is no need to accept the above listing as a straight line phylogenetic sequence. We might rashly hypothesize a sequence of increasingly complex behavior from *Lestes* and *Archilestes* to *Argia* and some *Enallagma* species, then a split leading to Calopterygids on the one hand and to species such as *Ischnura verticalis* wherein males apparently no longer maintain territory but instead seem to cruise about constantly

After *Argia apicalis* males established territory, they quickly seized females and it was apparent that they accurately discriminated sex and species. In our population, we never saw inter male pairing or mixed species pairs. Factors eliciting sexual pursuit vary among the species; in some, motion of female models is required, in others it is not. Males of *Argia apicalis* advanced sexually toward conspecific dead females pinned to a stick whereas males of *A. plana* never did so. BUCHHOLTZ (1956) reports a similar situation for *Platycnemis*. Males of *dealbata* advanced toward motionless female models, but, in cooler climates, *pennipes* advanced sexually only when there was to and fro motion of the models. She (1951) also showed that motion was required for sexual advance of *Calopteryx* males to females, but, this time, the required motion was up and down rather than to and fro.

In 1951 and 1956, BUCHHOLTZ showed that the wings of *Calopteryx* were important sexual releasers whereas the head and thorax of *Platycnemis* served a crucial role. In 1958, KRIEGER & KRIEGER-LOIBL demonstrated that the distal pale spot at the tip of the female abdomen played an important releasing role in *Ischnura elegans*. In a series of experiments, we (1965b) showed that a female thorax and one wing was the minimum stimulans required for release of sexual response in males of *Argia apicalis*, and that painted modifications of the color pattern of the female thorax reduced the frequency of male sexual response. LIEFTINCK (1956) describes the strikingly distended and colored 8th and 9th abdominal segments as well as the dilated and colored femora of certain Megapodagrionid species. He hypothesizes that these modifications function in recognition and courtship.

CORBET (1963) considers that male courtship apparently occurs in three zygopteran groups: Chlorocyphidae (*Rhinocypha*, *Libellago*, *Platycypha Chlorocypha*); Coenagrionidae (*Hemiphlebia*), and Calopterygidae (*Calopteryx*). The chlorocyphids display flattened tibiae in flight, *Hemiphlebia* displays abdominal appendages in resting males, and *Calopteryx* uses complex flight manoeuvres. Because the three methods are very different, it does not seem probable that the mere occurrence of courtship, without considering the precise type, can be used as substantial evidence of relationship. Courtship must have evolved several times. Interestingly, FRASER (1926, 1949), LIEFTINCK (1934) and PINHEY (1967) record that the display of the flattened tibiae serves for courtship in Chlorocyphidae, whereas HEYMER (1966) found that an apparently similar display served only for inter male aggressive display in *Platycnemis*. In the U.S., courtship, involving complex flight manoeuvres, has been demonstrated only for *Calopteryx maculata* (JOHNSON, 1962a), but I am confident that it occurs in the four other Nearctic species. In Japan, ASAHINA & EDA (1960) record courtship in *Calopteryx cornelia*, and, in Europe, PAJUNEN (1966) and HEYMER (1971) show that a complex courtship pattern occurs in the four *Calopteryx* species. Undoubtedly, courtship is widespread in the genus.

Female refusal movements occurred in only three of the species which we studied, and all three species oviposit primarily unaccompanied. The movements of Calopteryx maculata and the related Hetaerina americana (JOHNSON, 1961) are essentially the same. The females spread their wings as in wing warning and simultaneously bend their abdomens dorsally. In contrast, Ischnura verticalis females refuse males by curving their abdomens ventrally while their wings are spread. In 1937, GRIEVE stated that this action attracted males, but in 1963 CORBET considered it remarkable that this activity for attraction so closely resembled postures used in aeshnid females to escape males. In 1966, we designated this Ischnura activity as wing warning abdominal curving (WWAC), and from many movie records showed that it did not attract males, but rather warded them off.

Recently, EDA (1960), SCHMIDT (1965), HEYMER (1967b) discussed phylogeny of oviposition behavior. We hesitate to place our information in any of their outlines because of the extreme plasticity of oviposition behavior in most of the species we studied. Table 1 summarizes this variability. Archilestes grandis (BICK, 1970) oviposited nearly always in tandem, sometimes in the Lestes position and sometimes high in trees in an inverted position which we designate here informally as the Archilestes position. But, as for many other species, one female oviposited alone after her mate left. Each of the three species of Argia and Enallagma civile oviposited in both the Agrion and Sympecma positions. Variation was outstanding in Enallagma exsulans (BICK & HORNUFF, 1966) where four major oviposition patterns occurred within one population and where, during one oviposition sequence, one pair assumed three of the four patterns.

Discussing variability in the Order as a whole, CORBET (1963) states, "Indeed facultative behavior is the rule rather than the exception in many of their important activities." More recently, PAULSON (1969) states, "Behavioral polymorphism exists not only within a given species but also within a given individual, ... all evidence suggests that the strongest selection working on these insects has been that which increases the incidence of facultative behavior in individuals." We believe that an even greater range of variation occurs in almost every species than has hitherto been recorded and, that only quantitative data based on continuous observation of many pairs will reveal the true extent of the variation.

We sometimes generalize too hastily on generic behavior. Among our 12 species, three genera seemed constant in major aspects of oviposition behavior. But, is it safe to generalize for these ? We found that Calopteryx maculata (BICK, unpub.) oviposited exclusively at the surface, whereas JOHNSON (1962a) records that Calopteryx aequabile, sympatric with maculata in much of the U.S., descended beneath the surface. In other areas, ASAHINA & EDA (1960) photographed submerged oviposition in the unaccompanied female of Calopteryx cornelia; BUCHHOLTZ (1951) figured a female of Calopteryx splendens ovipositing alone beneath the surface; HEYMER (1971), generalizing for four European species, stated that females either remain at the surface or descend; and PAJUNEN (1966) showed that a single population of Calopteryx virgo oviposits submerged or at the surface depending on population density. Our population of Ischnura verticalis oviposited entirely alone, but HEYMER (1967b) states that Ischnura elegans occasionally oviposits accompanied by the male.

Table 1. Variation in oviposition behavior of some Nearctic Zygoptera. P- primary, S- secondary, =- data do not permit either primary or secondary designations.

	A. grandis	L. disjunctus	L. unguiculatus	A. apicalis	A. plana	A. moesta	E. aspersum	E. civile	E. exsulans	I. verticalis	H. americana	C. maculata
Tandem												
♀ not completely submerged												
Archilestes type	P											
Lestes type	S	P	P									
Agrion type				P	P	P		P				
Sympecma type				S	S	S		S				
♀ completely submerged									#			
♂ & ♀ completely submerged		S				S			#			
♀ alone; ♂ guards												
♀ not completely submerged												P
♀ completely submerged						S	P	S	#		P	
♀ alone; ♂ does not guard												
♀ not completely submerged	S	S	S	S	S					P		
♀ completely submerged									#			

In our population of Hetaerina americana (BICK & SULZBACH, 1966), the unaccompanied female always descended and JOHNSON's (1961) observations agree, yet KELLICOTT (1895) records incomplete submergence. LOIBL (1958) states that the majority of Lestes sponsa pairs oviposited above the surface, but she records nine submergences, one pair for 27 min. ROBERT (1958) also records submerged oviposition for sponsa, as does ANDOH (1969) who photographed a submerged pair and recorded that submergence lasted for 3-15 min. Lestes disjunctus (BICK, 1961) oviposited primarily above the surface, yet, during a period of high water, we recorded eight submerged pairs. European species of Platycnemis oviposit above the surface (HEYMER, 1966), but OBANA (1968) records that the Japanese P. foliacea once descended for 15 min. Correct interpretation of some of these examples is difficult because one cannot differentiate routine from exceptional behavior, and one seldom knows what peculiar environmental or behavioral circumstances were associated with the event.

IV. Problems

I will now mention matters that have concerned us, present problems, and ask questions which I hope will stimulate discussion.

There is an important problem of translation. Here, U.S. workers are often at fault because, lacking facility with languages, many direct most of their attention to English publications. But, the problem is general. Most citations are those written in the author's native language even when there is extensive pertinent literature in other languages. Certainly, most odonatologists neglect the numerous Japanese articles. However, even within a single language terms are used interchangeably without definition simply to avoid repetitious writing. An example is the words breeding, pairing, mating.

Odonate behavior, especially its territorial aspects, needs a more uniform terminology. Sometimes, we write about the same event under different terms, sometimes of different events under the same term. JOHNSON (1962a) records "wing flaps" in males of Calopteryx maculata and his description indicates similarity to "wing claps" in the species we have studied. Is it possible that the terms are different but the events the same ? Our "patrol flights" (=flight no reason) differ from FURTADO's (1970) "patrol displays" in the Oriental Amphipterygid, Devadatta, yet the terminology could suggest considerable similarity. An odonate's "settling base" within a territory differs from just any "perch site", yet the two terms sometimes seem to be used interchangeably. The terms: territory, home range, zone, neutral zone are troublesome, particularly so in translation. Recently many terms have been used when referring to groups away from water. We have: communal dormitory (HEYMER, 1971), just plain dormitory (GAMBLES, 1971), roosting aggregations (BEATTY, 1963), just plain aggregations (HEYMER, 1966), syngium for female aggregations and synandrium for male (HEYMER, 1966). We should make more effort to avoid giving rise to ethological homonyms and synonyms.

The printed word and even sequential diagrams drawn from movies inadequately depict much of behavior. There is no substitute for the film itself. Exchange of film, the informality of letter communication, personal conversation prior to publication are all much needed.

In spite of KORMONDY's (1961), JOHNSON's (1964), and ST. QUENTIN's (1964) discussions of territory, we still do not have a widely accepted definition applicable to all odonates. Criteria for territory often center around behavior, size, and localization, but the three can scarcely be considered separately.

Many workers stress behavioral criteria when they adopt NOBLE's (1939) traditional definition of territory as any defended area. But, can an odonate defend simply by being there, i.e., can the defense be by passive occupancy as may be the case in *Lestes disjunctus* ? A common requirement of territory is defense by aggressive behavior. PAJUNEN (1966) defined aggressive behavior as that "which clearly functions in restricting the range of other individuals or displacing them from a given area." What of the species which wing warns and flies toward intruders, yet often loses and is displaced as was the situation in *Lestes unguiculatus* (BICK & HORNUFF, 1965) ? Such a species engages in defense activity, but the effort seldom succeeds and the area is often lost. Certainly, we cannot expect that every defense activity will displace every intruder. Furthermore, maintenance of territory varies with population size. PAJUNEN (1966) *Calopteryx virgo* males in the same population were territorial when density was low, non-territorial when it was high. KLOTZLI (1971) has confirmed this; and HEYMER (1971) indicated its general occurrence in the other European *Calopteryx* species.

Size, when considered strictly alone, is seldom considered an important territorial requirement. But, can the territory be as small as 20 cm in diameter as we (1963) have used the term for *Enallagma civile* ? Could the territory be as small as a single stem, and, if there is no limit on size, just when does territory stand apart from minimum distance maintained ? Since BUCHHOLTZ (1955) and ZAHNER (1960) showed that size of territory in *Calopteryx* varies inversely with number of males at water, it is clear that demographic information would be most helpful whenever we inquire about size of territory.

The next question is, is localization required ? If so, how restrictive in space and time. Must a male return to precisely the same small area or will the same margin of the pond be sufficient ? What of duration ? ZAHNER (1960) stated that truly territorial males returned to the same territory after absences of three days, but neither KORMONDY (1961) nor JOHNSON (1964) considered duration important.

Definitions of basic reproductive terms are often troublesome. Mating, pairing, breeding are often used when copulation seems to be the intent of the author, yet one cannot be certain. This has given us trouble when tabulating literature records of copulation time. Does the statement, mating lasted as long as three hours, necessarily mean that copulation was that long, or was oviposition included? The word breeding is particularly vague. To some, it includes almost every aspect of adult behavior, and JOHNSON (1961, 1962a) uses the term in this broad sense in his papers on Breeding Behaviour in *Hetaerina* and *Calopteryx*; to others, it indicates entirely different matters, e.g., YAMAGUCHI's (1960) paper on Breeding in *Orthetrum* deals entirely with larval development. I think that the terms breeding, pairing, mating should not be used in any formal presentation dealing with detail. If copulation is meant we will have to say just that, or copula, or the wheel position; if oviposition is meant, we will have to say just that or deposition of eggs. If we use mating, or pairing, or breeding we will not be understood.

The placement of sperm (or is it a spermatophore ?) on the secondary genitalia of the male is generally designated as sperm transfer. However, there are many kinds of sperm transfer, and all differ from the event odonatists designate by that phrase. There is the internal transfer from one part of the male body to another, the transfer from male to female, and various transfers within the female body. In the Symposium on Insect Reproduction, HINTON (1964) discusses all these passages of sperm in his paper titled Sperm Transfer in Insects. Obviously, HINTON and odonatists are not referring to the same event even though both use the same term. Hoping to avoid confusion with other types of transfer of sperm, in 1970 and 1971a, we introduced the phrase, intra-male sperm translocation. This phrase may still confuse, but is seems much more restrictive than sperm transfer.

HEYMER (1967c) proposed a coordination of some aspects of odonate terminology. Coordination is much needed and should be one of the goals of conferences such as this. However, some of his proposals present difficulties. He uses eclosion and newly hatched where, I think, many workers would use emergence and teneral. Much confusion is caused by the word eclosion which is used for the appearance of both the first larval stage and the winged stage. Personally, I would limit the word eclosion to the appearance of the first larval stage. Also, I am certain that "newly hatched" generally suggests the first larval stage rather than the newly appeared winged stage as HEYMER clearly intended it. I do not fully understand what is wrong with the old and widely used term teneral for the newly emerged imago. Teneral may not be precisely delimited, but it will be more generally understood than HEYMER's use of "newly hatched".

The other difficulty in the HEYMER proposal involves differentiating the three kinds of winged odonates, i.e., his "newly hatched", "subadult", and "adult". His intent is to have a mutually exclusive terminology useable in field behavior studies. Undoubtedly, the newly emerged individuals, i.e., tenerals or "newly hatched" are recognizable as such for about the first day, but I question that HEYMER's criteria will clearly differentiate his subadults from adults without dissection or without prior knowledge of details of color change in a particular species. For example, KYLE (1959, 1961) did not recognize the age of specimens of Ischnura pumilio until he obtained expert assistance with dissection. He then learned that his specimens were immature and obtained evidence that the variety aurantiaca is merely an immature color phase.

Let me point out difficulties we have experienced. We (1965b) showed that in one population, females of Argia apicalis occurred in three color phases: brown, blue, and gray-black. Individuals in all phases were mature since they were in tandem, copulating, or ovipositing when marked. However, these certainly mature brown females look very much like recently emerged individuals. Confident determination of the sexual maturity of the brown females was practically impossible without dissection or prior marking.

The difficulty of distinguishing immature and mature individuals is particularly acute when they are away from water. Reproductive adults, after leaving water at sunset, do not return regularly the next day. We showed that sexually mature adults of disjunctus (1961), civile (1963), apicalis (1965c), and plana (1968) spend one or more days of their reproductive spans away from water, even during daylight hours. When subadults and adults resemble each other closely one cannot assume that all individuals away from water in the middle of the day are sexually immature.

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