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THE SUBGENUS *PERSICARGAS* (IXODOIDEA, ARGASIDAE, *ARGAS*)

11. Ecology and seasonal dynamics of *A.* (*P.*) *arboreus* Kaiser, Hoogstraal & Kohls in Egypt[1]

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Abstract: *Argas* (*Persicargas*) *arboreus* Kaiser, Hoogstraal & Kohls forms dense populations on trees supporting rookeries of the Cattle Egret, *Bubulcus i. ibis* (Linnaeus) in the Nile Delta and Valley and nearby oases. Ticks bred in spring and summer during the egret nesting season. At this time, larvae and nymphs were the most abundant stages. When birds abandoned the rookery in autumn, larvae and first-instar nymphs disappeared. Later nymphal instars survived the winter. Adults constituted the major part of the winter population, but no oviposition occurred. The life cycle of ticks reared experimentally under outdoor conditions took 2-3 months in Cairo area summer weather. In winter oviposition ceased, fed larvae failed to molt, and nymphal premolting periods increased significantly. There were 2–4 nymphal instars. Males passed through fewer instars than females before the final molt. Survival periods for each developmental stage were determined. Survival of the tick population depends on the prompt return of host birds to their regular breeding colony in the spring.

Argas (*Persicargas*) *arboreus* Kaiser, Hoogstraal & Kohls (1964) infests herons and other medium-size wading birds in many areas of Africa (Hoogstraal tick collection, unpubl. data). This tick is a host of a bacterium, *Salmonella typhimurium* (Floyd & Hoogstraal 1956) and of a rickettsialike microorganism, *Wolbachia persica* (Suitor & Weiss 1961). It is also naturally infected with Quaranfil and Nyamanini viruses (Taylor et al. 1966, Hoogstraal 1966, Kaiser 1966a, b). Quaranfil virus was first isolated from a febrile child living in a village a few kilometers from the site of the field study described in this paper. Elsewhere in Africa, other arboviruses, as yet unreported, have been isolated from this parasite (Hoogstraal, pers. commun.).

Results of experimental laboratory rearing (Kaiser 1966c) produced questions regarding the behavior and seasonal dynamics of *A.* (*P.*) *arboreus* in nature. This investigation is part of a worldwide effort to define the ecology, biological features and vector capability of *Argas* (*Persicargas*) species (Hoogstraal 1970).

In Egypt, *A.* (*P.*) *arboreus* commonly inhabits rookeries of the Cattle Egret, or Buff-backed Heron, *Bubulcus i. ibis* (Linnaeus). This conspicuous bird of the Nile Valley and Delta and nearby oases has been strictly protected since 1912, when its numbers became very low (Kirkpatrick 1925, Meinertzhagen 1930). The Cattle Egret is now a familiar part of the rural scene as it follows farmers and animals in fields to feed on insects, rodents, toads, and frogs that are disturbed by human and animal movement. This bird has recently found its way from Africa to the Americas, where its feeding habits (Burns & Chapin 1969) are similar. Earlier claims that the Cattle Egret feeds on ticks (Whymper 1909) have been discounted by Kirkpatrick (1925) and Hoogstraal (1956). Since this bird is beneficial to agriculture in Egypt, the subject of its relationships to parasitic ticks and tickborne viruses assumes special local importance. Owing to the wide distribution of *Bubulcus i. ibis* in Africa and warmer areas of North America, this study provides a baseline for comparative investigations in numerous other biotopes. *Argas* ticks are not known to infest the recently established Cattle Egret population in North America, but several species potentially capable of doing so are present on this continent (Kohls et al. 1970).

Bubulcus i. ibis characteristically nests in colonies or rookeries close to or in Egyptian villages. Flocks congregate in selected groups of trees to build or repair nests and to raise their young (Taylor et al. 1966). They normally disperse between late August and October and return to the rookery in late March or April of the following year. The destination of migrating adult and immature birds has not been investigated.

Few other hosts of *A.* (*P.*) *arboreus* are known in Egypt. A Mediterranean Hooded Crow, *Corvus corone sardonius* Kleinschmidt, harbored a female tick near Mit Abu Ghalib, Damietta (Kaiser et al. 1964). The Red Sea Reef Heron, *Egretta gularis schistacea* Ehrenberg, supports this parasite in a mangrove swamp rookery about 20 km south

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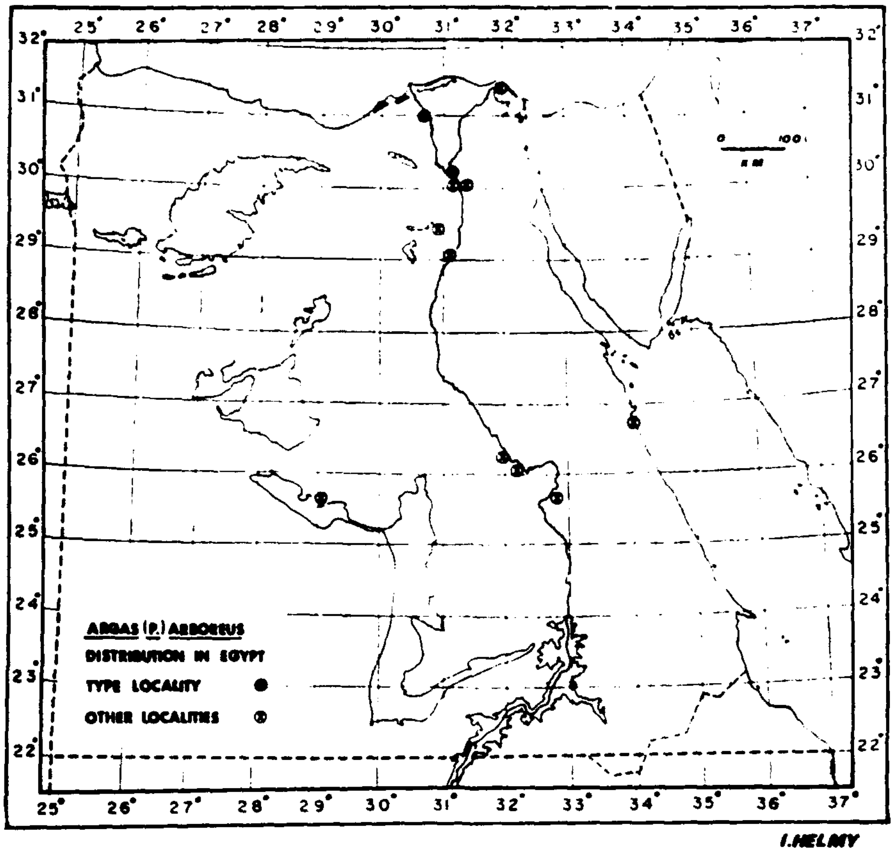

FIG. 1. *Argas* (*P.*) *arboreus* distribution in Egypt.

of Safaga, Quseir (Hoogstraal, pers. commun.).

This tick has been collected from the rookeries of *Bubulcus i. ibis* in the following Egyptian localities (FIG. 1): Delta Barrage Park (Qalyubia Governorate) (TYPE LOCALITY), El Horreya Gardens (Cairo Governorate), Zoological Gardens (Giza Governorate), Minshat el Biddini, Ihnasya el Madina (Beni Suef Governorate), El Kaabi, Sinnuris (Faiyum Governorate), Barkheil, El Balyana (Sohag Governorate), Minshat el Aammari, Luxor, and Aulad Nigm Bahgura, Nag Hammadi (both Qena Governorate), and El Hindaw, Dakhla Oasis (El Wadi el Gedid Governorate) (Hoogstraal tick collection, unpubl. data).

MATERIALS AND METHODS

Field investigations were made in the Delta Barrage rookery, Qalyubia Governorate [type locality of *A.* (*P.*) *arboreus*]. Collections were taken once each month from November 1966 to October 1968 during morning (1000–1200) hours. At each visit, 8–10 trees supporting *Bubulcus i. ibis* nests were examined from ground level to a height of ca 2 m. Ticks were brushed from cracks and under loose bark into a small metal tray and placed in test tubes. In the laboratory, they were sorted to stage and sex and counted. The different nymphal instars, except unfed N_1, could not be counted separately owing to their great similarity. Samples of associated arthropods were collected and identified. Ticks observed on the ground near trees were not counted.

To study the life cycle under natural climatic conditions, adults from the type locality were used to start a colony. Each tick was reared in a separate polyethylene tube closed at 1 end by a plaster of Paris plug and covered by muslin at the other end. The tubes were put in paper cups in outdoor shade beside the NAMRU-3 Medical Zoology laboratory. Hosts were domestic pigeons; feeding methods were those of Kaiser (1966c). After feeding, a male and a female were placed together and observed for oviposition. Adults were allowed to feed following each oviposition.

RESULTS

The Nile Delta Barrage rookery

Environment. The Nile Delta Barrage rookery [the type locality of *A.* (*P.*) *arboreus*, Kaiser et al. 1964, FIG. 40] is located in a large park at the apex of the Nile Delta about 18 km north of Cairo (FIG. 1). Across the river on both sides of the park, continuously-cultivated farms extend for the entire length of the Nile Valley and Delta. Trees grow along the margins of these farms and are numerous in the park.

The rookery is constructed on several species of trees identified (with English and Arabic common names) as: *Jacaranda acustifolia* (Bignoniaceae), Jacaranda (Jacaranda); *Casuarina stricta* (Casuarinaceae), Australian pine (Caswarina); *Terminalia arjuna* (Combretaceae), Indian almond (Terminalia); *Pinus longifolia* (Coniferae), Chir pine (Sonober); *Acacia nilotica* (Leguminosae), Nile acacia (Sant); *Cassia fistula* (Leguminosae), Golden shower (Khiar shamber); *Dalbergia sissoo* (Leguminosae), Sissoo (Sarsou); *Poinciana regia* (Leguminosae), Royal poinciana (Boinciana); *Ficus infectoria* (Moraceae), Lacor (Teen infectoria); *Eucalyptus citriodora* (Myrtaceae), Spotted gum (Kafur limoni).

TABLE 1. Arthropods associated with *Argas* (*P.*) *arboreus* population in the Nile Delta Barrage rookery.

INSECTA
- Coleoptera
  - Dermestidae
    - *Dermestes maculatus* DeG. (adults, larvae, & pupae)
    - *Attagenus gloriosae* (F.)
    - *Anthrenus verbasci* (L.)
    - *Anthrenus* 2 spp. (larvae)
  - Tenebrionidae
    - *Alphitobius diaperinus* (Panzer)
    - *Tribolium castaneum* (Herbst)
    - *Curimophena villosa* Haag-Rutenberg
    - *Ptinus variegatus* Rossi
  - Melyridae
    - Malachiinae; Genus?
    - Genus? sp.? (larva)
  - Ostomatidae
    - *Tenebrioides* sp.?
- Hymenoptera
  - Formicidae
    - *Crematogaster* sp.
    - *Pheidole* sp.
  - Braconidae
    - *Apanteles* sp. (Lepidoptera larval parasite)
- Lepidoptera
  - Tineidae
    - Genus? sp.?
- Hemiptera
  - Homoptera
    - Aphididae
      - *Aphis craccivora* Koch
  - Heteroptera
    - Reduviidae
      - *Coranus* sp. (nymph)

ARACHNIDA
- Acarina
  - Glyciphagidae
    - *Ctenoglyphus* sp. (immature)
  - Acaridae
    - Genus? sp.? (immature)

ARANEIDA
- Oecobiidae
  - Genus? sp.? (immature)
- Hersiliidae
  - Genus? sp.? (immature)
- Filistatidae
  - *Filistata* sp. (immature)
- Theridiidae
  - *Steatoda* sp. (immature)
- Gnaphosidae
  - ?*Herpyllus* sp. (immature)
- Thomisidae
  - *Xysticus* or *Oxyptila* sp. (adult and immature)

Sparrows, Palm Doves, Hooded Crows, Hoopoes, and other birds inhabit trees in the parks but apparently seldom visit the rookery.

Arthropods collected along with ticks belong to orders Hemiptera, Isoptera, Lepidoptera, Hymenoptera, Coleoptera, and Diptera, together with spiders and mites (TABLE 1). Most feed on organic debris, some on plant or arthropod fluids.

Climatic data (mean monthly temperature and RH) were obtained from the Imbaba Weather Station near the field study locality (TABLE 2). In 1967, the highest mean maximum and minimum temperatures were 35 °C (June, August) and 21 °C

TABLE 2. Climatic conditions near Nile Delta Barrage field study locality [A] and life cycle study locality [B], November 1966 to October 1968.*

	Temperature (°C)				RH	
	Mean Min.		Mean Max.		Mean	
Month	[A]	[B]	[A]	[B]	[A]**	[B]
1966						
Nov.	15.1	16.6	27.9	27.6	70	66
Dec.	9.1	10.7	21.6	20.7	57	53
1967						
Jan.	5.1	7.2	19.3	18.5	59	57
Feb.	6.8	9.0	20.3	19.8	59	55
Mar.	8.1	10.3	21.9	21.0	52	49
Apr.	12.0	14.2	28.8	28.2	46	42
May	15.5	17.5	30.8	30.1	51	49
Jun.	18.5	20.5	35.3	35.0	43	41
Jul.	20.5	21.7	34.3	34.1	56	55
Aug.	20.9	22.5	35.2	35.1	60	56
Sep.	18.7	20.7	32.8	32.4	59	56
Oct.	15.7	18.0	30.1	29.5	57	54
Nov.	11.9	13.6	25.1	24.2	60	60
Dec.	8.5	10.5	22.0	21.3	60	56
1968						
Jan.	6.8	8.8	18.9	18.1	59	51
Feb.	6.4	9.1	21.7	20.9	59	52
Mar.	8.4	11.0	23.3	22.7	—	48
Apr.	12.2	15.3	29.6	29.1	—	43
May	16.4	18.3	34.1	33.6	—	46
Jun.	19.9	22.0	36.0	35.9	—	45
Jul.	20.4	22.5	35.1	35.2	—	55
Aug.	19.6	21.4	34.2	34.0	—	55
Sep.	18.1	20.3	32.9	32.5	—	55
Oct.	15.1	17.2	29.2	28.6	—	55

*Data from Meteorological Department Weather Section, [A] Imbaba Station, [B] Abbassia Station.

**RH data not available from March to October 1968.

(July, August), respectively, and in 1968, 36°C (June) and 20°C (July), respectively. The lowest means were in January of both years (19 and 5°C in 1967, and 20 and 7°C in 1968). The 1967 mean RH was highest in January and lowest in June (RH data for 1968 were not available).

Host movements. An extraordinary modification of the normal cyclic pattern was observed during the monthly visits to the Nile Delta Barrage rookery between November 1966 and April 1967. The birds did not leave the rookery as usual in late summer of 1966. They remained on the nests, laid eggs, and successfully reared fledglings through the winter and during spring and summer to September 1967, after which they dispersed as usual. The reason for this exceptional winter residence and breeding in the rookery could not be determined. Climatic conditions (TABLE 2) were within normal limits. The 1968 season was uneventful, with birds returning in late March, fledglings appearing in early May, breeding continuing to the end of August, and the colony dispersing in late September and early October.

Tick population dynamics

Each developmental stage of *A.* (*P.*) *arboreus* congregated in any available crack or under loose bark on the lower 2 m of tree trunks (area examined) supporting rookery nests. Larger numbers were present on trees with deep crevices (e.g., *Acacia nilotica*) or loose bark (e.g., *Eucalyptus citriodora*) than on those with shallow or no crevices (e.g., *Dalbergia sissoo, Poinciana regia*). Ticks from the ground were not included in monthly counts but all stages, especially fed larvae and unfed first-instar nymphs, were observed close to trees beneath dry leaves, stones, bricks, and other debris.

Monthly examination revealed enormous tick numbers throughout the year regardless of season or presence or absence of the host. However, there was a clear seasonal difference in developmental stage composition of the collections (FIG. 2, TABLE 3).

Larval population. Unfed larvae clustered around the mother adult or were scattered with fed larvae, nymphs, and adults on the tree trunk. Larvae were present in the colony from May of each year to September in 1967 and October in 1968. They comprised 2.1–14.2% of the total tick collections. Maximum larval incidence was 10.3 and 14.2% in July 1967 and 1968, respectively, at which time the host was nesting, the mean minimum temperature was 15.1–20.9°C, mean maximum 2[illegible]–36.0°C, and mean RH 43–60%. Early in Oct[illegible] when the birds began to disperse, no larvae [illegible] found.

Nymphal population. Nymphs comprised 13.6–

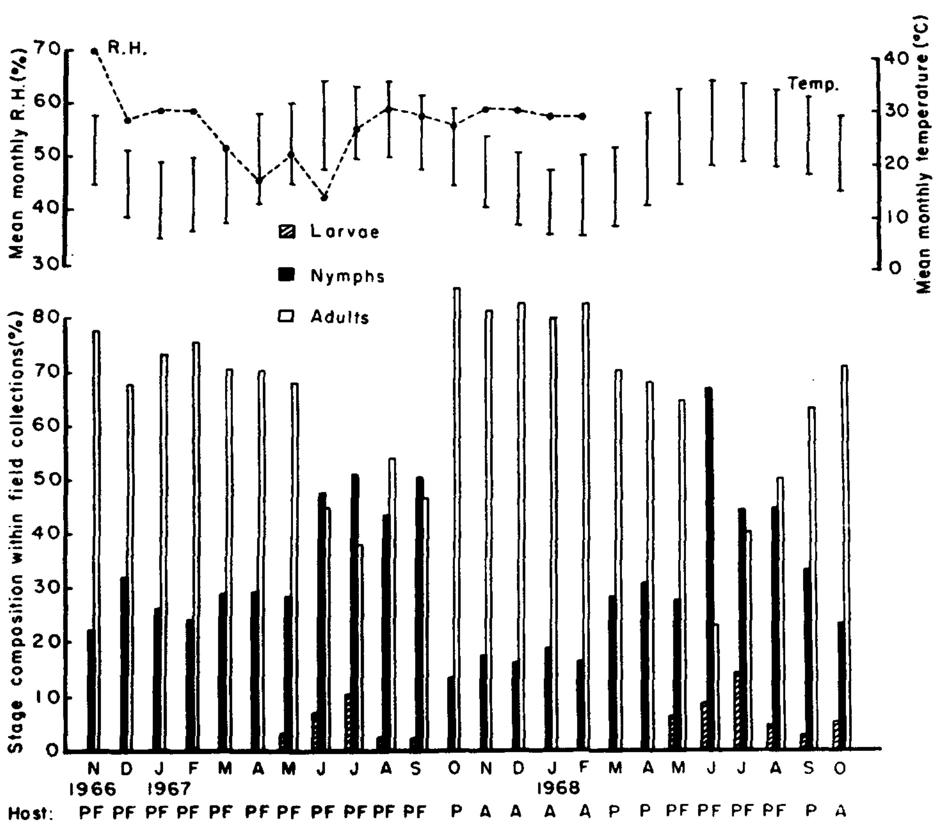

FIG. 2. Monthly developmental stage composition of *Argas* (*P.*) *arboreus* population in Nile Delta Barrage rookery, November 1966 to October 1968, in relation to host presence and climatic conditions (RH data not available from March 1968). A = hosts absent. F = fledgling hosts present. P = adult hosts present.

TABLE 3. Adult and immature stage numbers of *Argas* (*P.*) *arboreus* population in Nile Delta Barrage rookery, November 1966 to October 1968.

MONTH OF COLLECTION	TOTAL TICKS	LARVAE NO. (%)	NYMPHS NO. (%)	♀♀ NO. (%)	♂♂ NO. (%)
1966					
Nov.	324	0	72 (22.22)	122 (37.66)	130 (40.12)
Dec.	436	0	140 (32.11)	144 (33.04)	155 (35.55)
1967					
Jan.	467	0	123 (26.34)	166 (35.55)	178 (38.11)
Feb.	532	0	128 (24.06)	187 (35.15)	217 (40.79)
Mar.	373	0	108 (23.95)	107 (28.69)	158 (42.36)
Apr.	409	0	120 (29.34)	91 (22.25)	198 (48.41)
May	363	11 (3.03)	103 (28.37)	89 (24.52)	160 (44.08)
Jun.	469	33 (7.04)	225 (47.97)	88 (18.76)	123 (26.23)
Jul.	466	48 (10.30)	240 (51.50)	80 (17.17)	98 (21.03)
Aug.	387	8 (2.07)	169 (43.67)	89 (23.00)	121 (31.26)
Sep.	487	10 (2.05)	248 (50.93)	99 (20.33)	130 (26.69)
Oct.	295	0	40 (13.56)	129 (43.73)	126 (42.71)
Nov.	410	0	73 (17.80)	128 (31.22)	209 (50.98)
Dec.	589	0	96 (16.30)	212 (35.99)	281 (47.71)
1968					
Jan.	299	0	57 (19.06)	120 (40.14)	122 (40.80)
Feb.	267	0	44 (16.48)	100 (37.45)	123 (46.07)
Mar.	309	0	89 (28.80)	104 (33.66)	116 (37.54)
Apr.	277	0	86 (31.05)	57 (20.58)	134 (48.37)
May	289	18 (6.23)	81 (28.03)	89 (30.80)	101 (34.94)
Jun.	385	34 (8.83)	262 (68.05)	40 (10.39)	49 (12.73)
Jul.	618	88 (14.24)	278 (44.98)	84 (13.59)	168 (27.19)
Aug.	687	31 (4.51)	313 (45.41)	168 (24.46)	176 (25.62)
Sep.	535	14 (2.62)	179 (33.46)	166 (31.03)	176 (32.89)
Oct.	726	36 (4.96)	170 (23.42)	252 (34.71)	268 (36.91)

68.0% of the total collections. Indices were highest during the host nesting season, June to September in 1967 (43.7–51.5%) and June to August in 1968 (45.0–68.0%). Most nymphs molted to adults in August and September before hosts departed. Consequently, between October 1967 and February 1968 nymphal indices decreased to between 13.6 and 19.1%. Wintering nymphs (except unfed first-instar) survived till hosts returned in March, when they fed and molted to the adult stage. In the same period of 1966–1967, the slightly higher (22.2–32.1%) nymphal indices may have been related to the unusual wintertime presence of herons in the rookery.

First-instar nymphs were recorded from June to November in 1967 and from May to October in 1968. During these periods, monthly mean minima were 11.9–20.9 °C, mean maxima 25.1–36.0 °C, and mean RH 43–60%. Unfed first-instar nymphs survived only about 2 months following host departure. During the host breeding season, first-instar nymphs appeared soon after newly hatched larvae (May–June).

Adult population. Adults were represented in all monthly collections and comprised 23.1–86.4% of the total ticks collected. The high adult proportion at the end of the tick breeding season (86.4% in October 1967, 63.9% in September 1968) continued at this level for 8–9 months. During this period, the mean temperature minima were 5.1–16.4 °C, mean maxima 18.9–34.1 °C, and mean RH 46–70%. At the beginning of the following (spring) breeding season, adult indices decreased and immature stages formed the major part of the colony.

Males were more numerous than females, especially in April of 1967 and 1968, when this sex comprised 48.4% (each year) and females 22.2 and 20.6%, respectively, of the total collections (TABLE 3). Of the 6625 adults taken throughout the study, 2908 were females and 3717 were males (sex ratio 1.00: 1.28).

Ovipositing females rested along the entire examined length of the tree, with no apparent preference for lower or higher parts. Females brooded eggs [as described by Hoogstraal (1953, 1956) for other argasid species] from April to September each year. At this time, hosts were nesting, the mean temperature minima were 12.0–20.9 °C, mean maxima 28.8–36.0 °C, and mean RH 43–60%. Females that fed in late summer or early autumn did not oviposit until the following spring. No ovipositing females were observed from October 1966 to April 1967, even though the birds exceptionally nested in this winter period and abundant food was available for the ticks.

Life cycle

To explain certain phenomena observed in the *arboreus* population in nature, a detailed life cycle study was made under natural climatic conditions outside the NAMRU-3 Medical Zoology laboratory a few kilometers from the Nile Delta Barrage rookery. Data for the first adult feeding and oviposition followed a constant pattern. Those for all other feedings and ovipositions did not differ significantly from each other; thus they are grouped under the term "subsequent" and compared with the first group of data.

The life cycle from oviposition to adult emergence was completed in 45–100 days in the summer weather of Cairo area (TABLE 2, 4).

Oviposition. From May to August, females started ovipositing 5–23 (mean 14.3) days following the first meal and completed this process in 5–17 (mean 10.1) days. These intervals were shorter for subsequent ovipositions, being 3–11 (mean 5.8) and 3–19 (mean 8.9) days, respectively, in May and June, and 3–8 (mean 4.6) and 4–12 (mean 8.2) days, respectively, in July and August.

No oviposition occurred in autumn and winter (October to March). Each of 18 newly molted and old females that had fed in September (6) and October (12) delayed oviposition until the following spring. Twelve of these females oviposited in April and May; the other 6 fed again in late April and oviposited in May and June. The preoviposition period for these 18 females was 178–269 (mean 216.8) days and the oviposition period was 7–17 (mean 11.9) days.

Daily egg output was irregular except in the last 2–3 days of the oviposition period when the numbers gradually decreased. Oviposition occasionally diminished or ceased for 1–2 days. The mean daily output of 2.2–12.5 (mean 7.6) eggs for the first oviposition was significantly greater in subsequent ovipositions, being 6.3–20.0 (mean 10.6) in May and June and 5.1–20.5 (mean 13.1) in July and August. The mean daily output of females with a prolonged preoviposition period was 3.4–9.5 (mean 10.3) eggs.

Total egg numbers per female were 11–143 (mean 82) and 23–234 (mean 101) for the first and subsequent ovipositions, respectively. Females deposited 243-1781 (mean 681) eggs in 3–15 (mean 6.7) batches during their 80–842 (mean ca 14 months) day life span.

The egg incubation period was 15–18 (mean 15.8) days in May, and 11–15 (mean 12.6) days in August.

Larval stage. Unfed larvae survived for 18–34 (mean 25.0) days in May and June, 12–24 (mean 18.1) days in July and August, and 22–49 (mean 33.8) days in February and March.

Larvae attached to the host 3–7 (mean 4.3) days after hatching. In August, engorged larvae dropped after 4–10 (mean 6.1) days and molted 5–7 (mean 5.9) days later. The cool weather of December and January prolonged these periods to 6–11 (mean 7.6) and 52–65 (mean 57.5) days, respectively, and also reduced larval viability. In winter, 18 (60%) of 30 fed larvae died during the premolting period, and 6 (20%) were unable to escape from their exuviae and died during molting. The remaining 6 larvae molted to weak first-instar nymphs that could not feed when placed on the host and died within a week after molting.

Nymphal stage. There were 2–4 nymphal instars. Of 27 F_1 adults, 3 (11.1%) molted from N_2, 23 (85.2%) from N_3, and 1 (3.7%) from N_4.

Unfed N_1 survived 10–56 (mean ca 1 month)

TABLE 4. Duration of life cycle periods of *Argas* (*P.*) *arboreus* reared outdoors in Cairo summer weather*.

Developmental stage	Prefeeding	Feeding: Days	Feeding: Minutes	Premolting	Preoviposition	Oviposition
Larva	3–7 (4.3)	4–10 (6.1)		5–7 (5.9)	—	—
$Nymph_1$	3–11 (3.9)		13–77 (27.0)	6–9 (6.9)	—	—
$Nymph_2$	1–10 (4.2)		10–130 (29.4)	8–9 (8.7) (to ♂)	—	—
				8–11 (9.2) (to N_3)	—	—
$Nymph_3$	3–11 (5.3)		13–80 (38.3)	10–14 (12.2) (to ♂)	—	—
				10–17 (12.8) (to ♀)	—	—
				10 (to N_4)	—	—
$Nymph_4$	7		33	13 (to ♀)	—	—
♂ (1st)	2–19 (7.0)		20–65 (44.7)	—	—	—
(subsequent)	10–59 (27.5)		10–120 (44.8)	—	—	—
♀ (1st)	2–17 (8.8)		20–90 (45.3)	—	5–23 (14.3)	5–17 (10.1)
(subsequent)	1–12 (3.0)		12–120 (52.1)	—	3–8 (4.6)	4–12 (8.2)

*All periods are in days except for feeding of post-larval stages. Means are in parentheses.

days in summer and 14–72 (mean ca 1-1/2 months) days in autumn. Unfed N_2 and N_3 survived for significantly longer periods, 72–352 (mean ca 8 months) and 103–451 (mean ca 9 months) days, respectively.

N_1–N_4 fed 1–13 days after molting (means 3.9, 4.2, 5.3, and 7.0 days, respectively); feeding periods were 10–130 minutes (means 27.0, 29.4, 38.3, and 33.0, respectively). Coxal fluid was usually emitted a few minutes after full engorgement and detaching from host. Occasionally, the fluid was emitted on the host during the last few minutes of feeding.

In summer, N_1–N_4 molted 6–9 (mean 6.9), 8–11(mean 9.1), 10–17 (mean 9.1), and 13 days, respectively, after feeding. Intervals for nymphs molting to adults were almost similar to those of nymphs molting to subsequent instars. In winter, the significantly longer nymphal premolting periods were 94–103 (mean 99.3), 92–110 (mean 100.1), and 98–116 (mean 106.8) days for N_1–N_3, respectively.

Adult stage. Of the 27 F_1 adults, 13 were males and 14 were females (sex ratio 1.00: 1.08). However, this ratio differed greatly for adults emerging from N_2 (1.0: 0.0), N_3 (1.0: 1.3), and N_4 (0.0: 1.0).

Maximum survival of unfed males and females was approximately 2 years. Longevity was 162–697 (mean ca 14 months) days for males and 142–710 (mean ca 13 months) days for females.

Adults first fed 2–19 days after molting. Subsequent feedings were 1–12 (mean 3.0) days after completion of oviposition in females, and 10–59 (mean 27.5) days from the previous meal in males. Feeding periods for both sexes were 10–120 minutes, but males usually became replete faster than females.

DISCUSSION

Argas (*P.*) *arboreus* population dynamics in nature appear to be affected by 4 interrelated factors: (1) climate, (2) presence or absence of hosts, (3) longevity of each developmental stage, and (4) diapause. The necessity for diapause and hence the survival capacity of fed and unfed stages is determined by both climate and the presence or absence of hosts. Results of experimental studies on each of these 4 factors will be reported separately. The present paper concerns only data and observations from a tick population in its natural habitat and from rearing samples from this population in natural climatic conditions.

Climate usually (not always) affects the host nesting period and host departure from and return to the rookery. Springtime return of the host allows overwintered ticks to feed, resulting in oviposition in late April and appearance of F_1 larvae in May. In the early summer months of June and July, immature stages compose the major part of the tick population, but by August adult numbers begin to increase. These data coincide with those of the life cycle study, in which larvae developed to adults in about 2 months. In late summer, host birds normally abandon the rookery, immature ticks are no longer produced, and the ratio of adult to immature stages in the tick population increases significantly.

Winter and summer temperature and RH extremes in this rookery appear to be well within the limits of *arboreus* tolerance. However, in winter all larvae die and nymphal premolting periods are longer than in summer.

The effect of the survival capacity of each *arboreus* developmental stage on the population dynamics is clearly demonstrated by the absence of unfed larvae soon after the bird hosts depart and of first-instar nymphs 2 months later. Other instar nymphs and adults can survive without food throughout the winter. These field observations coincide with the life cycle data, in which the mean survival period for unfed larvae, N_1–N_3, females, and males was 1, 1-1/2, 8, 9, 13, and 14 months, respectively. Thus, tick population survival in nature depends on the punctual return of hosts to established rookeries each spring (Kaiser 1966c).

Field observations and life cycle data under natural conditions revealed a tick breeding season of 5–6 months during which 1 or 2 tick generations were produced. A 6–7 month resting period followed. During this rest, the tick population consisted of N_2, N_3, and adults. Nymphs that fed in late summer continued slow development with long premolting periods (ca 2 months for N_1, 3–4 months for N_2 and N_3). Engorged females entered diapause, oviposition ceased, and no eggs or larvae were produced until the following spring.

The alternate summer breeding and winter resting seasons of the tick persisted in nature even when the host modified its migratory habits and wintered in the rookery during the winter of 1966–1967. In the life cycle study, the tick activity pattern remained unchanged even though a host was regularly available for feeding during winter.

Notably, no *arboreus* ticks were observed on trees near those composing the rookery. The observation of more unfed larvae on tree trunks than on the ground agrees with the observation that unfed newly hatched larvae are negatively geotropic

(Hoogstraal 1956). However, fed larvae were often found under debris on the ground near trees. The high ratio of males to females in the monthly collections may be attributed to longer male survival. Egg production and more rapid digestion of the blood meal, as observed in our histological studies (to be published), may cause females to have a shorter life and to die more quickly than males.

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