

## PROGRESS REPORT

### Filoha Hamadryas Project / Awash Baboon Project

Awash National Park, Ethiopia

October 2015

Herein we report research carried out by members of the Filoha Hamadryas Project, a subsidiary of the Awash National Park Baboon Research Project (ANPBRP), otherwise known as the Awash Baboon Project, co-directed by Clifford Jolly and Jane Phillips-Conroy. The research of the **Filoha Hamadryas Project (FHP)** is carried out exclusively on hamadryas baboons, *Papio hamadryas hamadryas*, at the Filoha outpost of the Awash National Park, and is coordinated by Larissa Swedell.

Because we did not submit a progress report in 2014, this progress report covers a two-year period, from mid-2013 to mid-2015.

### 1. PROJECT OBJECTIVES

The objectives of the Awash Baboon Project as a whole are to gather and disseminate information on the behavior, ecology, morphology, anatomy, and genetics of olive (anubis) baboons, hamadryas baboons, hybrid baboons, and grivet monkeys found in Awash National Park. Most broadly, the objectives of the Awash Baboon Project are to expand scientific knowledge of the non-human primates of Ethiopia, including biological knowledge basic to the conservation and management of wild primate populations. In addition, the project aims to promote the development of the science of primatology in Ethiopia, especially by providing field and laboratory training for professional and pre-professional biologists.

At present and for the past 15 years, the Awash Baboon Project consists exclusively of research carried out by the Filoha Hamadryas Project on hamadryas baboons, *Papio hamadryas hamadryas*, at the Filoha outpost of the Awash National Park. The goals of the Filoha Hamadryas Project are to investigate the ecology, behavior, endocrinology, and genetics of the hamadryas baboons as a means to elucidate basic principles of socioecology, the adaptive value of social behavior, the evolution and maintenance of hamadryas baboon social organization, and the ecology of semi-desert habitats so as to contribute to our understanding of ecology, evolution, and sustainability.

*The current members of the Filoha Hamadryas Project (FHP) are:*

Larissa Swedell (Director and Coordinator of FHP)

Kumara Wakjira Gemeda (Local Counterpart/Project Associate)

Teklu Tesfaye Abebe (Senior Field Assistant)

Alex Amann (PhD Student)

Michaele Lemons (Field Assistant)

Katarina Evans (PhD Student)

### 2. FHP RESEARCH 2013-2015:

For most of the period covered by this progress report, we have not been able to collect behavioral data due to several transitions in our field team, illnesses of members of our team, and large gaps in observation due to difficulties finding the baboons. In July 2015 we were finally able to fit three (3) satellite collars on adult males and this has improved our ability to track the baboons. We also now have a more consistent field team in place with the arrival of PhD student Alex Amann in June 2015.

We are currently focusing on two main lines of research, **(1)** the adaptive value of social bonds and **(2)** the interacting reproductive strategies of males and females.

### **Background 1: Hamadryas Social Organization**

The hamadryas social system is characterized by four levels of social structure: the *troop*, *band*, *clan*, and *one-male unit* (Kummer 1968, 1971; Abegglen 1984; Swedell 2006; Schreier & Swedell 2009). *Troops* occur when bands aggregate at common resources but are not otherwise cohesive or consistent social entities. A *band* shares a common home range and generally coordinates its movements. Within bands are *clans*, defined based on patterns of association among males, who tend to stay in their natal clan (Sigg et al 1982; Schreier & Swedell 2009; Staedele et al 2015); members of clans physically resemble one another and appear to be close kin (Abegglen 1984; Pines et al 2011; Staedele et al 2015). Finally, within bands and clans are *one-male units* (OMUs) of one adult 'leader' male, adult females, dependent offspring, and sometimes one or more 'follower' males. Most social interactions occur within OMUs, the cohesion of which is maintained by aggressive herding behavior of leader males (Swedell and Schreier 2009). As a result, leader males have nearly exclusive sexual access to the females in their OMUs (Kummer 1968; Abegglen 1984; Swedell and Saunders 2006). Also within bands and clans are 'solitary' males, which move throughout the band, do not associate regularly with any one OMU, and maintain social relationships with other males and juveniles (Pines et al 2011).

Unlike other baboons in which philopatric females form the stable core of the social group, hamadryas are characterized by kin bonding among largely philopatric males, who control female behavior (Kummer 1968; Abegglen 1984; Colmenares 2004; Swedell and Schreier 2009; Pines et al 2011; Swedell et al 2014). Males occasionally disperse from their natal clans (though more often remain in them) to search for receptive females, and females are forcibly dispersed among OMUs by males (Sigg et al 1982; Swedell & Schreier 2009; Swedell et al 2011, 2014). This results in female-biased gene flow among hamadryas populations (Hapke et al. 2001, Hammond et al. 2006; Staedele et al 2015). Hamadryas females thus have fewer opportunities for interactions with kin due to male-imposed dispersal (Swedell & Schreier 2009; Swedell et al 2011, 2014). Despite this reduction in kin bonding potential, behavioral data suggest that hamadryas females do forge and maintain intrasexual relationships, albeit highly variable in strength (Swedell 2002, 2006). Because females are transferred one at a time, the occurrence of kin dyads within OMUs likely varies widely and it is this variation that probably underlies at least some of the observed variation in patterns of affiliation among females (Swedell 2002, 2006; Colmenares 2004).

Hamadryas social organization is thus multi-layered, with affiliative bonds operating at multiple levels. Within OMUs, strong *cross-sex bonds* tie each female to her leader male. *Female social bonds* vary in strength, perhaps according to degree of kinship (Swedell 2002, 2006; Colmenares 2004). Leader and follower males within OMUs rarely interact except via formalized greetings, but hamadryas social units as a whole appear to be linked via *male social bonds* at the clan level (Abegglen 1984; Swedell and Schreier 2009). The hamadryas system thus includes female-female bonds within (and occasionally between) OMUs, male-female bonds within OMUs, and male-male bonds within clans and possibly bands (Kummer 1968; Abegglen 1984; Swedell 2002, 2006; Colmenares 2004; Pines et al 2011, 2015).

### **Background 2: Hamadryas Reproductive Strategies**

Darwin (1871) outlined how sexually dimorphic morphology and behavior could evolve via intersexual mate choice and intrasexual mate competition. Trivers (1972) followed this theoretical groundwork with a focus on parental investment, such that males are predicted to attempt to maximize their number of mates and offspring, while females, who invest more energy into a more limited number of offspring, are predicted to focus more on offspring quality and be more demanding than males with regard to mate selection. As an outcome of the process of sexual selection, males and females in some species have become sexually dimorphic as males compete amongst each other over access to females, which selects for larger body size and canine size. This sexual dimorphism occurs mainly in polygynous mating systems that involve female defense (Clutton-Brock 1984; Plavcan and van Schaik 1992). In more polyandrous and polygynandrous mating systems, males may compete indirectly through queuing and sperm competition (Harcourt et al. 1981; Anderson and Dixson 2002; Marty et al. 2009; Dubuc et al. 2011; Fujii-Hanamoto et al. 2011).

The differing interests between males and females can and do lead to *sexual conflict*, wherein the strategies of males are at odds with those of females, which can lead to sexual coercion (Smuts and

Smuts 1993; Clutton-Brock and Parker 1995) and infanticide (van Schaik 2000; Hausfater and Hrdy 2008). Sexual coercion occurs when a male behaves aggressively towards a female in order to increase the chances that she will copulate with him, at a cost to the female. Aggression by males towards females in the context of mating attempts has been documented in chimpanzees, macaques and baboons (Berenstein and Wade 1983; Lindburg 1983; Goodall 1986; Manson 1994), while actual forced copulation has been observed in gorillas, chimpanzees and orangutans (Nadler and Miller 1982; Galdikas 1985a, b; Mitani 1985; Nadler 1988).

Hamadryas baboons (*Papio hamadryas hamadryas*) are arguably the most sexually coercive of non-human primates (Smuts and Smuts 1993; Clutton-Brock and Parker 1995). Leader males aggressively move individual females among social units and in fact benefit from these takeovers, in that the more females a male transfers into his unit the more offspring he is likely to sire (Swedell et al. 2014). These coercive transfers carry a cost for females, however, due to increased risk of infanticide and lengthened interbirth intervals (Swedell et al. 2014).

While sexual selection and parental investment theory predict that males will attempt to maximize their number of offspring (Darwin 1897; Trivers 1972), even at a cost to female fitness (Parker 1979, 2006), we also expect selection to have shaped female behavior so as to mitigate any fitness costs imposed by males (Hrdy 1977, 1979). Indeed, female mammals may use a variety of counterstrategies to male coercion and infanticide, including paternity confusion through pseudoestrus and termination of investment in offspring that are likely to die anyway as a result of infanticide (van Schaik 2000; Hausfater and Hrdy 2008). We therefore expect female hamadryas baboons to possess strategies to mitigate the costs to their fitness imposed by hamadryas males.

### ***Major Objectives***

Our current major objectives within **Research Area 1, the adaptive value of social bonds**, are to (1a) quantify *patterns of social bonding* within and between the sexes, (1b) determine the *fitness benefits of social bonds*, and (1c) assess the role of *kin selection* in shaping social behavior in hamadryas baboons. Our major objectives within **Research Area 2, the interacting reproductive strategies of males and females**, are to determine whether hamadryas females (2a) use *pseudoestrus*, i.e., anovulatory (“deceptive”) sexual swellings post-takeover, to confuse a male’s assessment of female reproductive condition, (2b) *terminate pregnancies* post-takeover to curtail maternal investment and save energy in the face of infanticide risk, and (2c) experience heightened *stress* during takeovers, a potential proximate mechanism for these two potential physiological strategies. To answer these questions, we will need to collect and analyze behavioral data in concert with genetic and hormonal data.

### ***Research Activities to Achieve Objectives***

For many years now we have been collecting samples from both male and female hamadryas baboons for **genetic analysis** in order to ascertain kinship relationships. Genetic kinship among wild hamadryas baboons had never been determined prior to our research and is important in order to address patterns of sex-based dispersal as well as the role of kin relationships in patterns of behavior. These samples are collected following the methods of Nsubuga et al. (2004) and are sent to Dr. Linda Vigilant’s laboratory in the Department of Primatology at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany. Genetic analysis of these samples has been ongoing in Dr. Vigilant’s laboratory at Max Planck for the past four years.

We have also continued to collect fecal samples for **hormone analyses**. These samples are collected using a method developed for hormone extraction and preservation under field conditions (Beehner & Whitten 2004) and are transported to Dr. Jacinta Beehner’s laboratory at the University of Michigan. Our hormone samples are currently still awaiting analysis in Dr. Beehner’s laboratory.

In addition to genetic and endocrine data, we have been continuously collecting **demographic data**, i.e., movements among social units, as often as possible. We have also collected **behavioral data** as often as possible but due to the above-mentioned personnel shifts and gaps in observation behavioral data have not been prioritized during the period covered by this progress report.

### 3. FHP RESEARCH OUTPUTS 2013-2015:

- Swedell, L. (2013) Hamadryas Baboon (*Papio hamadryas*). IN *The Mammals of Africa, Vol. 2, Primates*. edited by T. Butynski, J. Kingdon, & J. Kalina. London: Bloomsbury Publishing, pp. 221-224.
- Swedell, L., Leedom, L., Saunders, J., & Pines, M. (2014) Sexual conflict in a polygynous primate: costs and benefits of a male-imposed mating system. *Behavioral Ecology and Sociobiology* 68: 263-273 (DOI: 10.1007/s00265-013-1641-3).
- Amann, A., Pines, M., & Swedell, L. (2014) Female takeovers in hamadryas baboons: Consequences and counterstrategies. *American Journal of Physical Anthropology Supplement* 58: 66 (poster at 2014 annual meeting of the American Association of Physical Anthropologists).
- Chowdhury, S., & Swedell, L. (2014) Factors affecting turnovers and takeovers in chacma and hamadryas baboon societies. *American Journal of Physical Anthropology Supplement* 58: 94 (poster at 2014 annual meeting of the American Association of Physical Anthropologists).
- Pines, M., Chowdhury, S., Saunders, J., & Swedell, L. (2015) The rise and fall of leader males in a multi-level society: takeovers and tenures of male hamadryas baboons. *American Journal of Primatology* 77: 44-55 (DOI: 10.1002/ajp.22309).
- Städele, V., Van Doren, V., Pines, M., Swedell, L., & Vigilant, L. (2015) Fine-scale genetic assessment of sex-specific dispersal patterns in a multilevel primate society. *Journal of Human Evolution* 78: 103-113 (<http://dx.doi.org/10.1016/j.jhevol.2014.10.019>).
- Staedele, V., Vigilant, L., & Swedell, L. (2015) Female friendships in a 'non-female-bonded' cercopithecine: genetic correlates of sociality and female choice in hamadryas baboons. *American Journal of Physical Anthropology Supplement* 60: 296 (poster at 2015 annual meeting of the American Association of Physical Anthropologists, St. Louis, MO).
- Chowdhury, S., Pines, M., Saunders, J., & Swedell, L. (2015) The adaptive value of secondary males in the polygynous multi-level society of hamadryas baboons. *American Journal of Physical Anthropology* 158: 501-513 (DOI: 10.1002/ajpa.22804).

### 4. FHP FINANCIAL CONTRIBUTIONS 2013-2015:

#### Foreign Researcher Fees:

Since the implementation of the new EWCA policy requiring research fees for foreign researchers, we have paid a research fee of USD 1000 per foreign researcher per year to EWCA. In 2013 this totaled \$4,000 for Megan Cole, Luke Nolby, Samantha Patterson, and Eila Roberts. In 2014 this totaled \$1,000 for Anna Schier, and for 2015 so far this has totaled \$4,000 for Alex Amann, Kristin Crouse, Katie Spencer, and Michael Lemons. This totals **\$9,000** for the two-year period covered by this progress report.

#### Rent for Use of House at Filoha:

As has been standard in the past, we have paid **birr 320 per month** to the Awash National Park for the use of one of the four round houses at the Filoha outpost. We use the house for storage and as a kitchen.

#### Salaries for Park Scouts:

As usual, park scouts are hired to accompany researchers when following baboons. This totals about **\$150 per month**.

#### Mammals of Africa 6-Volume Set:

Drs. Thore Bergman, Jacinta Beehner, Peter Fashing, and Larissa Swedell (of this project and two other projects affiliated with EWCA) jointly purchased a newly published six-volume set *Mammals of Africa* for donation to EWCA, and this was delivered to EWCA by Jacinta Beehner on our behalf in September 2014. This set is valued at nearly **\$800**.

## **5. FUTURE PLANS FOR FINANCIAL CONTRIBUTIONS AND TRAINING:**

### Hands-on Field Training and Per Diem:

We will be happy to provide hands-on field training in the collection of behavioral and ecological data from wild primate populations to any EWCA personnel that would like to join us at Filoha during our field seasons. As per our agreement, the project would pay a per diem of birr 70 per day for each day spent in the field.

Prepared by Larissa Swedell

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