Arabian Babblers adopted as fledglings are accepted as mates by their adopters (unlike offspring, which are not taken as mates)

Avishag Zahavi, Naama Zahavi-Ely and Tirtza Zahavi, October 11, 2021

(Avishag Kadman-Zahavi) This is not a formal article, but rather a sharing of findings and of questions about the phenomenon of Arabian babblers that were adopted as fledglings by another group. The material was gathered during my work in cleaning up errors and adding details to the database of observations from the Arabian babbler study at Hatzevah, Israel, that was started and led from 1971 to 2017 by my late husband, Professor Amotz Zahavi, and is still ongoing. The changes and additions in the data were always verified by written notes taken at the time of observation – I never relied on memory alone. But memory helped me look for and find details that were observed and noted in writing at the time, but not entered at the time into the database. This work is intended to consolidate the relevant data and bring the questions to the attention of researchers of babblers and of others interested in animal behavior.

Thanks to my daughters, Naama and Tirtza, who recognized the importance of the subject matter, encouraged me to consolidate and analyze the data, and put in significant time in helping me work with diminished eyesight.

.

Topic

Arabian babblers do not copulate with any individual who was a member of their group when they hatched, including of course their parents, or with any individual that was hatched in their group while they were members of it. On the other hand, they do copulate with individuals that were hatched in another group and adopted by the group as nestlings or fledglings (that is, under 6 months of age, when they still beg for and receive feedings by adults). This indicates that babblers know and remember which individuals they may copulate with and which they may not, even years after the differentiating event. This in turn indicates long-term individual recognition of specific individuals.

Introduction:

We have encountered "adoptions" by babblers -- that is, observations of the fledglings of one territorial group spending time with another, neighboring group. Usually the fledglings return to their original group, but sometimes they stay permanently with the other group. We call this phenomenon "adoption." Members of the adopting group accept the visiting fledglings, feed them and take care of them as if they were their own young. There is no observable difference between the way adults treat such adopted fledglings and the way they treat their group's own offspring. But in one respect there

is a fundamental difference: in future years, some of the adopted individuals copulate with their adoptive parent. Out of 42 cases of adoption, 25 survived to over 1 year of age; out of these 25, there were 6 cases in which a babbler adopted as a fledgling mated (that is, formed a breeding pair) with its adoptive parent, and two more in which a babbler adopted as a fledgling copulated with its adoptive mother, but did not become the dominant male in the group (see table 3). One should note that in order for such a mating to occur, several fairly rare coincidences have to occur: 1. The adopted babbler needs to survive to at least one year of age, 2. The dominant of the same gender needs to be gone from the group, and 3. There must be no older adult of the same gender as the adopted individual in the group, except for descendants or siblings of the remaining dominant (who are not accepted as mates, as stated above). In fact, in every case where such circumstances occurred, the adopted babbler mated with its adoptive parent.

The avoidance of matings of parents and offspring or siblings is particularly clear in groups where all breeding activity ceased for considerable periods, sometimes for over a year, when all group members were parents and offsprings or siblings of each other: the adults in the group prevented outsiders of their own gender from entering the group, and did not breed with one another. Table 5 lists 12 such cases.

The study of the Arabian babblers at Hatzevah was started in 1971. The individuals in the study area are tame, and trained observers can spend time among them with minimal interference with their natural behavior. The landscape is a very open, arid savannah that facilitates observations as well. Each babbler is identified by colored rings on its legs – three colored rings and one metal ring with its individual number.

Babblers live in permanent territorial groups of between 2 and 20 individuals. Each group territory has only one nest, and breeding is limited almost entirely to the dominant member of each gender. Adult babblers that did not hatch in the group can only join as a rule by replacing the current adult group members of the same gender. The newcomers – one individual or a coalition of individuals of the same gender – chase away any adult member of the group of the same gender, and become the reproducing dominant members. Rarely, an adult individual joins a group without aggression as a subordinate, particularly if the current dominant needs support against strong neighbors. Any adult that joins a group can potentially mate with any individual of the other gender that is in the group at that time. Fledglings that join a group, on the other hand, are accepted by the group smoothly and are sometimes actively enticed by members of the group (we have also seen some cases where a young babbler accompanied an adult babbler that joined a group).

For more information in general about the 50-years-long Arabian babbler study at Hatzevah, see publications by Amotz Zahavi and others.

The current study shows clearly that adopted babblers, who come from another group, are treated as potential mates even if they join the group as young fledglings in need of

feedings. This indicates that babblers recognize and remember years later who they may mate with and who they may not.

Methods and results

The data used in this study was extracted out of the database of observations that were conducted regularly at the study center at Hatzevah. Over the years of study, data was collected for individuals and for groups. Data for individuals include the group and date of hatching and/or ringing, changes in social ranking, moves to another group or becoming a floater, the last date it was observed, and other data. Data for groups include group members and their social ranking at any given time, plus breeding activities and dates. This study consolidates cases where babblers that hatched in one group moved to another group as fledglings (that is, under 6 months old). We pulled out from written field observations additional details about these adopted individuals, particularly those that lived longer or achieved breeding.

Table 1: all adopted individuals that were identified in the database

Name	Name	ID	Sex	Age reached	Natal	Adopting	Adopting Age	Adopting	Entrance	Story
				(Days	Group	Group	(days	Date	Туре	
				since	'	'	since		''	
				ringing			ringing			
				or			or			
				leaving			leaving			
0.4.7.4		5047	F4	nest)	D070	10.00	nest)	04/00/0044	Δ.	*
CATA	כאטא	5617	F1	1878	BSZ?	KVS	un	01/06/2014	Α	*
CHTS	כחטש	5729	F	549	TLM	HIL	64	31/07/2015	С	
CVVT	כווט	4758	F1	735	PDN	ZVA	un	10/04/2004	D	*
HHCT	חחכט	4938	F	785	SAL	BOK	34	24/08/2006	E	*
THSL	טחשל	5643	F	337	NIS	DOD	43	06/05/2015	В	
TLSS	טלשש	1921	F1	1686	BBS	TMR	58	21/07/1988	Α	*
TVPC	טופכ	5745	F	187	NIS	MCB	161	10/12/2015	В	
VLTC	ולטכ	2389	F	201	POL	TOK	51	08/08/1983	?	
ACTA	אכטא	5114	M1	2696	THS	ELU	90	15/09/2010	С	*
AGTZ	אגטצ	4705	M1	4353	???	BOT	Un	28/05/2003	Α	*
ATCA	אטכא	164	M1	2972	ZOM	STV	Un	07/06/1991	Α	*
CPLT	כפלט	5135	M1	3151	KAN	HIL	123	17/09/2010	С	*
CSVT	כשוט	3153	М	381	BOK	CNM	45	21/05/1994	?	
CTGS	כטגש	4706	M1	340+	???	BOT	Un	11/06/2003	С	*
GCTL	גכטל	4663	М	862	ATD	DOJ	Un	04/01/2003	Α	*
GHGT	גחגט	4982	M1	1671	SAL	BOK	Un	03/06/2006	Е	*
HATH	חאטח	5730	M1	1618	TLM	HIL	64	31/07/2015	С	*
MTLH	מטלח	3075	M1	1107	TOM	MIZ	141	05/07/1994	С	*
SHAT	שחאט	4760	М	662	PDN	ZVA	in the	10/04/2004	D	*
TA07		0047	N 4	4070	LINIO	CLID	nest	40/07/4004	^	*
TASZ	טאשצ	3217	М	1276	HNC	SHR	61	13/07/1994	A	,
TAZA	טאצא	5727	М	394	TLM	HIL	64	31/07/2015	В	
TCHH	טכחח	3172	M1	373	WSZ	DRB	81	06/07/1994	Α	*
THAV	טחאו	3076	М	600	TOM	MIZ	141	05/07/1994	С	*

TSGL	טשגל	4983	М	427	SAL	BOK	Un	03/06/2006	Е	*
TSMZ	טשמצ	2045	M1	2379	BOK	BMS	89	09/06/1979	В	*
VZLT	וצלט	2577	М	112	BTS	SHD	52	02/06/1978	?	
ZSTS	צשטש	5747	М	187	NIS	MCB	161	10/12/2015	В	
ZTZG	צטצג	5560	M1	1041	TLM	BER	45	16/07/2014	С	*
ZTZP	צטצפ	5537	M1	560	TLM	BER	75	16/07/2014	С	*
AVTV	אוטו	5228	U	6	SBT	MTE	5	08/05/2011	Е	*
CLTP	כלטפ	5848	U	92	KOT	TLM	68	01/08/2016	Α	
CSTC	כשטכ	5559	U	235	TLM	BER	52	16/07/2014	С	*
HPAT	חפאט	5558	U	59	TLM	BER	52	16/07/2014	С	*
LLTA	ללטא	961	U	343	KEN	STV	61	04/06/1984	?	
LTLS	לטלש	4761	U	11	PDN	ZVA	in the	10/04/2004	D	*
							nest			
LTPZ	לטפצ	5187	U	43	THS	ELU	34	17/09/2010	С	*
SSZT	ששצט	3757	U	323	???	DOJ	Un	11/02/1994	Α	
SVTC	שוטכ	4929	U	171	POL	HOR	30	01/08/2006	Α	*
TAZG	טאצג	5229	U	5	SBT	MTE	5	8/05/2011	E	*
THZL	טחצל	4759	U	11	PDN	ZVA	In the	10/04/2004	D	*
							nest			
TSHS	טשחש	5502	U	66	MTE	TPU	39	20/04/2014	Α	*
TZHS	טצחש	2237	U	163	BBS	TMR	7	24/06/1981	?	

M1, F1 = reproducing individuals; U = unknown gender (did not reach the age in which eye coloration changes in females)

Entry type: see table 2

Table 2: manner of entry into the adopting group

Entrance	n. cases		n. Ind	ividuals		Code
Туре		F	М	U	Total	
Alone	11	2	5	4	11	Α
With adult	4	1	3	0	4	В
with siblings	7	2	8	3	13	С
in the nest	1	1	1	2	4	D
Enticed	2	1	2	2	5	Е
Unknown	5	1	2	2	5	?
Total		8	21	13	42	

A – joined alone

B – joined with an adult (often the adult was not accepted, or left the group soon after; the fledgling stayed with the new group)

C – several fledglings from the same group joined another group together – some may have left later

D – a group took over the territory of another group that included an active nest, and took over raising the nestlings

E – we observed the adopting group actively enticing fledglings from another group to follow them, using movements and calls that are normally used for leading the group's own fledglings from one place

to another. In such cases, often the parents then enticed the fledglings to return to their home territories; such cases where the fledglings ended up in their original group are not included in this study.

Table 3: adopted individuals that achieved breeding

Age: days since leaving the nest. 7 out of the 34 were adopted in the nest (when the other group took over the territory), or were enticed away a few days after leaving the nest. 18 of the 27 others were adopted between 30 and 70 days from leaving the nest, and only 5 joined at an older age (120-161 days from leaving the nest).

Adopting groups: 6 out of the 24 groups that adopted fledglings were new groups, where the adoptions occurred while the group was being formed. In three of them, the adopted fledglings entered together with an adult from the same group of origin. Some of the other groups that adopted had lost individuals (adults or fledglings) a short time before adopting.

Male/female ratio among adopted individuals: table 1 shows that there are fewer females than males among the adoptees whose gender is known. We can tell the gender of babblers by the color of their iris: it is light in males and dark in females. Juvenile coloration is similar to that of females. The age of change varies between 3 and 9 months; thus, we usually can't tell the gender of individuals that did not survive to 9 months of age. Every path of adoption shows a higher ratio of males than females. The total number is low, though, so statistics may not be reliable.

Table 3 summarizes adoptees that became reproducing individuals, and the circumstances

										Breeding	Final
					Adopting	Adoption				age	age
Case	Name	Name	ID	Sex	group	date	Type of	f breed	er	(days)	(days)
		1	1	Ī			A*	B*	C*	Ι	
							^	В			
A1	CATA	כאטא	5617	F1	KVS	1/06/2014	+	+		308	1878
A2	CVVT	כווט	4758	F1	ZVA	10/04/2004	+	+		675	735
A3	TLSS	טלשש	1921	F1	TMR	21/07/1988		+		1271	1686
A4	AGTZ	אגטצ	4705	M1	BOT	28/05/2003	+	+	+	340	4353
A5	CPLT	כפלט	5135	M1	HIL	17/09/2010	+	+		462	3151
A6	ZTZP	צטצפ	5537	M1	BER	16/07/2014	+	+		439	560
A7	CTGS	כטגש	4706	M1	BOT	11/06/2003	+	+		>300	>340
A8	HATH	חאטח	5730	M1	HIL	31/07/2015	٨		+	720	1618
A9	TCHH	טכחח	3172	M	DRB	06/07/1994	٨			<373	373
A10	ATCA	אטכא	164	M1	STV	07/06/1991		+		733	2972
A11	ACTA	אכטא	5114	M1	ELU	15/09/2010		+		1081	2696
A12	GHGT	גחגט	4982	M1	BOK	03/06/2006		+		1212	1671
A13	ZTZG	צטצג	5560	M1	BER	16/07/2014		+		526	1041
A14	TSMZ	טשמצ	2045	M1	BMS	09/06/1979		+		1429	2379
A15	MTLH	מטלח	3075	M1	MIZ	05/07/1994			+	Un	1107

Table 3, Circumstances of breeding: A – with an adoptive parent B – in the adoptive group C – in another group A -- copulated with the adopting mother but did not become the dominant male in the adopting group.

Breeding results are summed up in table 4

				total	U	М	F	
Adoptees followed			42	13	21	8	מספר מאומצים מתועד	
Live	Lived over one- year			25	0	19	6	מתוכם חיו שנה או יותר
bec	became breeders			14	0	11	3	היו למתרבים
bred	bred in adopting Gr			12		9	3	התרבו בקבוצה המאמצת
bred	bred with Adopting parent		8		6*	2	התרבו עם הורה מאמץ	

^{*} Two additional males copulated with their adoptive mother, but did not breed with her

8 of the 25 adopted individuals that reached one year of age bred with, or at least copulated with, an adoptive parent – compared with thousands of potential cases of parent-offspring pairings that were avoided. Out of the adopted individuals that reached one year of age, 11 of the 19 males and 3 of the 6 females became breeders. This is a high ratio compared with the rest of the population, and is worth examining.

Table 5 lists groups where no breeding took place over a period of time when all group members were parents and offspring or siblings of one another – which can happen when one of a dominant pair is gone. In such groups, adult offspring of the dominant pair prevent other babblers of their gender from joining the group. The table lists the start and end dates of this state, the number of adult males and females that were in the group when it started, and the way it ended.

Table 5: no-breeding situations

	Group	Group	Missing	No l	present	at start	New members when ended		
	Code	name	gender	Start	End	Total days	М	F	Gender & number
ב1	BOK	בוקר	F1	03/05/2006	22/02/2007	295	4	2	1F
ב2	EST	מזרח	F1	03/01/1999	05/05/2000	488	4	1	3F
ב3	HAK	חקלאים	F1	02/01/1996	22/02/1997	417	4	2	1F
ב4	HNK	חנוכה	F1	09/07/1999	20/04/2000	286	6	4	1F
ב5	KEN	קן-חדש	M1	02/05/1987	01/02/1988	275	2	4	1M
ב6	MTE 1	מטה 1	M1	15/08/2005	11/06/2006	300	2	4	1M
7ב	MTE 2	מטה 2	F1	20/11/2011	13/02/2013	451	5	4	3F

ב8	MZR 1	-מזרח	F1	06/03/1987	24/02/1989	518	4	3	1F
		רחש 1							
ב9	MZR 2	-מזרח רחש 2	F1	24/06/1999	02/06/2000	344	3	2	2F
ב10	POL	פולשים	F1	10/12/1989	02/02/1990	54	2	4	1F
ב11	TLM	טלמים	M1	03/02/2005	27/03/2006	417	5	1	1F
ב12	TMR	תמרים	M1	18/09/1997	22/05/1998	246	5	2	1F

The twelve groups in table 5 were all stable groups of 5-10 adult babblers, that did not conduct breeding activity for long stretches of time. This table only grazes the surface of the topic, there may have been many more groups in similar situations. This phenomenon shows the high cost of avoiding breeding of parents with their offspring or among siblings by babblers.

Since the number of adoptees is small -- only 25 that reached a year of age -- and since each case is unique, we go into details of the stories of some of them (A1-A20). We also describe in detail how the situation was resolved in the case of groups with non-breeding combinations, in which also each case is unique (1B-12B).

A1: CATA of the KVS group

In August 2014, after several upheavals, the KVS group stabilized with a dominant male LVTP, a second male VSAT, an adult female ATLH, a fledgling daughter of VSAT named LATG, and an adopted female fledgling CATA. The two female fledglings grew up together, and VSAT's daughter ranked higher than the adopted one, as shown by allofeedings and by taking over guard positions. In January 2015 the dominant male disappeared, and VSAT became the dominant male. They tried breeding, but in early April the nest was destroyed and the dominant female disappeared. About two weeks later VSAT and the adopted female CATA started building a new nest. LATG, who was the daughter of VSAT and who was dominant over CATA, increased her gestures of dominance. In the Fall LATG was observed as a floater outside the group territory, and shortly after she disappeared. CATA and VSAT remained as the dominant pair in the KVS group until CATA disappeared five years later, in summer 2020. This is a classical case of avoiding father-daughter mating, even though the daughter was dominant over the adopted daughter. The adopted daughter became the breeding female, rather than the actual daughter that outranked her.

A2: Nestlings adopted in the nest: CVVT of the group ZVA.

In 2004, four nestlings were ringed in the nest of the PDN group (which consisted of an adult pair, male and female). A few days later the territory of the PDN group was taken over by the ZVA group. The parents of PDN were chased off, and the conquering group ZVA continued to take care of the PDN nestlings. The nestlings fledged out of the nest, one disappeared immediately and another shortly after. The two remaining fledglings did well as a part of the ZVA group. The adopting mother disappeared in mid-December 2005, and the adopted female nestling CVVT became the dominant female, with her adopting father GTVL. In February 2006, two females of the DOJ group took over the ZVA group and chased away CVVT, who was later

observed as a floater far away from the group's territory. We visited the group on that day and saw that the adoptive father GTVL, rather than joining the new females in building a nest, was standing on treetops at the border of the territory and calling loudly. We thought he was searching for CVVT. We did not see nesting activity between CVVT and her adopting father GTVL prior to that, but at that time of the year (December 2005 to January 2006) there was no breeding activity in any of the neighboring groups. All of them started breeding activities in the third week of February 2006, the same week that CVVT was chased away. Thus, we don't know for a fact whether CVVT, the daughter adopted as a nestling in the nest, was accepted as a potential mate or not.

A3: TLSS in TMR group:

TLSS was ringed in the BBS group, and adopted by the TMR group when she was three months old. At that time, the TMR group consisted of two males and a female, and had lost three fledglings shortly before. Soon after her adoption, her adopting father was chased away by her biological father (from the BBS group), and her adopting mother was replaced by a female new to the research area (a "barbarian"). TLSS grew up in the TMR group. Her biological father was chased away in the summer of 1991, and in the Fall of the same year TLSS became the breeding female of TMR. It should be noted that by this time, even though the group continued for years, none of the group members was an offspring of the group. This is a common situation.

A4: AGTZ and CTGS in the BOT group:

On May 26, 2003, the BOT group was made up of two males and a female; it was observed up the Shezaf wadi with a young unringed fledgling. Since the fledgling showed no fear of us, that is, it was tame (used to humans), we assumed that it was the unringed fledgling that was missing at that time from the SAL group. The fledgling was ringed as AGTZ; it was begging for food and was fed by all group members. In June we observed in the group another fledgling in addition to AGTZ, one that was not tame (=not used to humans). This fledgling was ringed as CTGS. The dominant female was observed incubating, and in July AGTZ took part in feeding the nestlings at the nest; CTGS was still shy of us and kept away from observers. The nestlings fledged out of the nest but did not survive. In October the second male in the group (GLTL) left the group and joined another that was forming nearby, but in December he returned to the BOT group and in February 2004 he chased away the dominant male and bred with the female. This nesting resulted in two female fledglings. In April 2004, the second adopted fledgling (CTGS) chased away GLTL, became the dominant male, and bred with his adopting mother; he disappeared in June 2004. At this point AGTZ was the only remaining male in the group. He also mated with his adopting mother, at an unusually young age. He appears again in stories 6b and 7b.

A5: CPLT at the HIL group:

The HIL group was made up of babblers that came from outside the study area ("barbarians") and included a male, a female, and a fledgling; they took over an excellent territory in the Gidron, next to the Ras Hashita campground and the date orchards of Boaz and of Elbaz. They got used to our presence quickly. On September 10, 2010, the fledglings of the nearby KAN

group who fledged from the nest on June 13, 2010, were spending time with the HIL group, and the HIL group members fed them. The next day, the KAN group parents came and led them back to their home group; over several days, the three fledglings moved back and forth between the two groups. In the end, CPLT stayed with the HIL group and the others returned to the KAN group. CPLT outranked the original fledgling that came with the HIL group, and the latter disappeared on April 25, 2011. On April 16, 2011 there was a nest with nestlings in the group. ATPA, the dominant male in the group, was lame and sick; only SSZT and CPLT fed the nestlings. CPLT also sat on the nest. Later on ATPA, even though he was sick and lame, was seen feeding the fledglings, though less so than the others. CPLT was observed opening his beak to ATPA, which is a sign of submission to ATPA's higher rank. Soon after ATPA started going every morning to the campsite's bathroom at Ras Hashita and attacked his reflection in the mirror so much that he got bloody. When the mirror was covered, he started attacking his image in the mirror of our jeep. His physical condition deteriorated, and on August 28, 2011 he disappeared. CPLT became the top-ranking male and bred with his adoptive mother. He remained the dominant male of the HIL group for many years, up to the writing of this chapter (April 5, 2020) – at one point he was chased away from the group and returned to it after some adventures, which are not connected to his being adopted and will be reported elsewhere.

A6: ZTZP and ZTZG at the BER group:

The BER group was formed in July 2014 in the middle of the northern area, comprised of TVSZ, a three-year-old female from the HIL group; LZVT, a young year-old male originally from the HOR group; another year-old male, ZTAL, TVSZ's brother, who disappeared a few days later; plus four ringed fledglings from the TLM group: ZTZP that hatched in April, and three that fledged in June 2014: ZTZG, CSTC, and HPAT. There were many chases between the BER group and neighboring groups, but they held on. They nested in March 2015 and in May 2015, and managed to raise fledglings, but only one survived of each brood. In early June LZVT disappeared, and the adopted ZTZP took his place as the dominant male, together with his adopting mother. ZTZP immediately started showing off dominance over his younger brother ZTZG, who opened his beak to him indicating recognition of his dominance. It was the end of the breeding season and thus ZTZP did not actually nest with his adopting mother. In September 2015 TVSZ was chased away by SPAT, who entered the BER group together with her two fledglings. ZTZP disappeared in October 2015 and his brother ZTZG, who was also adopted, became the dominant male until he disappeared in April 2017.

A7: CTGS at the BOT group – see 4a.

A8: HATH and TVAP at the HIL group:

HATH was adopted by the HIL group with his brother and sister – it seems that they joined the group on their own initiative, since the group had a fledgling of the same age (PAST, who disappeared in September 2015). HATH was raised by the group and is mentioned often in observations of the group, particularly the extended allopreening between him and his adopting mother TVAP. On April 5, 2017, the group had three fledglings, offspring of TVAP and CZCT (who drove out from the group his father KPLT). On April 23, 2017 CZCT was missing – he

was apparently driven out by HATH. HATH and TVAP started a breeding cycle right away but the nest was not successful. On May 23, 2017, KPLT, HATH's adopting father, was observed with his son CZCT in the eastern part of the territory; the female TVAP joined them and they started breeding right away. HATH remained in the western part of the territory, which included the Agricultural Research Station (MOP), and a female from a neighboring group joined him. Both groups, MOP and HIL, are still around at this date (February 2020).

A9: TCHH at the DRB group:

TCHH was observed copulating with his adopting mother when he was a year old. The female disappeared shortly after; his adopting father lived longer than he did, so he did not reach the rank of the dominant male in the group.

A10: ATCA at the STV group:

ATCA was ringed as a fledgling at the ZOM group. On April 19, 1991, when he was three months old, he was adopted by the STV group which in the previous summer had lost most of its members, including the breeding female. Five days after ATCA joined the group, two adult females joined it, from two different groups. After several days of clashes, the younger of the two chased away the older one and became the dominant female of the STV group. In April 1993 the dominant male (the adopting father) disappeared and ATCA became the dominant male in the STV group.

A11: ACTA at the ELU group:

ACTA was an offspring of the THS group, which consisted of two. He was ringed as a nestling on April 6, 2010, and left the nest a few days later. In May THS had another round of breeding and in July three fledglings left the nest – only one of them survived. On September 11, 2010, ACTA joined the ELU group (which consisted of two males and a female), and a few day after another fledgling joined him. The later was ringed at the ELU group as LTPZ. For several days the fledglings moved back and forth between the ELU and THS groups, until the THS group disappeared (last seen on September 26, 2010. On October 11, 2010, the adopting mother of the fledglings disappeared and a female from outside the study area took her place: TPLL. The younger fledgling disappeared as well. ACTA grew up in the ELU group with two other males outranking him. In January 2012 APTV, the dominant male, was chased away by his brother HHTS. A year later, in March 2013, HHTS was chased away by his adopted son ACTA (see more on HHTS and TSHS in story 17a). ACTA became the dominant, breeding male in the ELU group for many years.

A12: GHGT in the BOK group – the kidnapping of the fledglings of SAL group:

BOK was a simple group of a breeding couple (THHG as M1 and TSAL as F1), two daughters (ZATA and STLV), and three males of different ages. In June 2006 the breeding female TSAL disappeared in mid-nesting, and the group was left with no breeding combination (see table 5 and story 1b). The older daughter ZATA built a nest, laid eggs, and incubated them, but they had not been fertilized and did not hatch. Amotz removed the eggs eventually several weeks later; the next day, on June 3, 2006, two young fledglings who were used to us appeared in the

group, who disappeared from the neighboring SAL group. They were ringed as GHGT and TSGL, both of whom turned out to be males. A month later the group enticed another fledgling from the SAL group's subsequent nest, HHCT, who turned out to be a female. In December 2006 the oldest daughter, ZATA, disappeared, and two months later the biological mother of the three SAL fledglings, HTAZ from the SAL group, chased away the BOK adult daughter STLV and took her place. The morning before, we noticed the father THHG and his daughter STLV allopreening each other for a long time – as though they knew they would be separating. We were curious how the young sons would react to their biological mother joining the group. We saw both of them attack her – but it is common for babbler males to attack females. In September 2008 HTAZ was chased away by another female (THLV), and GHGT, who had left the group, rejoined it. Some time later, after the last of his adopting brothers disappeared, GHGT chased away his adopting father (THHG) and nested with the new female.

A13: ZTZG at the BER group – see A6.

A14: TSMZ at the BMS group:

TSMZ hatched in the BOK group, and moved to the BMS group as a fledgling together with an older brother. When he was three years old he left the group, but a year later he returned to it after his brother disappeared. He became the breeding male.

A15: MTLH and TCAV at the TOM group:

MTLH and his brother THAV hatched at the TOM group in Spring 1994. Five months later we found them at the MIZ group. We don't know whether they joined by their own initiative, or whether members of the MIZ group enticed them. In the month before they joined, the MIZ group lost four fledglings who hatched that Spring. In the following Spring, when they were a year old, MTLH and his brother joined a newly-forming group, MTT, together with a male from outside the research area, a two-years-old female from the ZVA group and two one-year-old females, also from the ZVA group. In the summer of that year the dominant male disappeared, and MTLH became the dominant male in the MTT group. His brother TCAV disappeared a few days afterwards.

Adoptees who did not achieve reproduction

A16: TASZ in the SHR group:

The SHR group formed in January 1994 by two brothers from the ZVA group and five females from the ROD group. Between February and May 1994 they built three nests with 6, 9, and 5 eggs respectively, a higher number than usual, indicating that more than one female was laying eggs, that is, a struggle among the females over reproduction. Only some of the eggs hatched. Overall, only five nestlings were ringed, and only one of them survived – a daughter that was ringed on May 8, 1994. At the same time, the neighboring HNC group was raising eight fledglings from two nestings, and three more from yet another nesting, one of them TASZ. During a fight between the groups, TASZ ended up in the SHR group. He was happy to stay

there as an adopted fledgling, together with the SHR daughter of the same age. TASZ became an adult and lived in the SHR group over three and a half years, but his adopting father had a long life, and TASZ did not end up in position to reproduce.

A17: GCTL in DOJ group:

GCTL was ringed as a nestling in a nest of the ATD group. On July 16, 2002, he was observed with the group in a greenhouse in Ein Yahav – this was the last time that the ATD group was observed. In January 2003 GCTL was observed with the DOJ group – we don't know where he was between July and January. He lived as a group member; his adopting parents survived him and he did not end up in position to reproduce.

A18: TSHS in the TPU group:

TPU was a new group that was chased away by all their neighbors. There were several days of indecision over the location of the next nest, with the female trying to build a nest at the Sheizaf wadi and the male gravitating to the Egel area in the hilly area south of the Sheizaf. The male (HHTS, who was chased out of the ELU group) tried to lead the female by the same motions that adults use for leading fledglings. In the end, the nest was built in the area that the male was interested in. TSHS hatched in the MTE group and was ringed in the nest on March 12, 2014, with three other nestlings. On April 7, 2014 their parents were already busy with a new nest. TSHS' older brother was observed attacking TSHS vigorously. Under the circumstances, he was happy to move to the TPU group where both adults fed him. PATL, a young female of the MTE group, tried to lead him back to his home group but apparently he preferred to stay as the only fledgling in the TPU group. He stayed in the TPU group until it disappeared after May 17, 2014.

A19: SVTC in the HOR group:

SVTC fledged in the POL group. On August 1, 2006, Amotz saw the month-old gledgling of POL remain with the HOR group. We don't know whether any member of the POL group tried to lead it back to its original group. We noticed that when it was with the HOR group, it was asking for food loudly and the adults often thrilled when feeding it. We assume that individuals acquire prestige by feeding others, and that the calls were intended to draw group members' attention to the feeding. SVTC disappeared at the age of five months, before we could tell what its gender was.

A20: the abduction of the fledglings of the SBT group by the MTE group:

In the Spring of 2011, MTE was a stable group that included a breeding pair, the five-years-old son of the dominant male, six one-year-old females, a year old male, and a fledgling of about 5 weeks. At the beginning of their next nesting cycle they roamed over the borders of their territory and encountered the SBT group, which had three young fledglings who had left the nest a few days earlier. The young females started enticing the fledglings, using sounds and movements typical of leading fledglings. Two of the three SBT fledglings responded and followed them. By nightfall, the fledglings did not reach the MTE roost tree but spent the night in a small bush half-way between the groups. The next morning the young females returned to

them and fed them. The older fledgling of the MTE group joined them and took over most of the food. Two days later one of the fledglings was not able to get to the top of the roost tree, and disappeared overnight. The second survived a few more days, but in the end was not able to get up to the night roost together with the group and did not survive either. The third fledgling of the SBT group, who remained with his home group, developed well and helped his parents raise the next generation of fledglings.

A21 adopting within the group: TVPA and his adopting mother:

Two weeks after TVPA and his three siblings fledged out of the nest at the HNC group, three females from the SAL group chased away the biological mother LVTA, and her two daughters GTZA and ALAT. The new females "adopted" and took care of the two-week-old fledglings. On June 31, 2007, when he was two years old and after his father and three-years-old brother disappeared, TVPA became the highest-ranking male in the HNC group, and the breeding female was GTZA who had raised him since he was a two-weeks-old fledgling. At the start of the next breeding season, on March 8, 2008, males from the MTE group took over the HNC group and chased TVPA away. Thus, TVPA was the dominant male in the HNC group only during a time when there was no breeding activity in any group. The question of whether he would have mated with the mother that raised him since such a young age remains open.

There are actually many cases of adults taking over groups that include young fledglings – most takeovers happen during breeding season. Such cases should be searched for in the data and examined.

<u>Details of situations where groups ended up with no acceptable breeding combination (table 5),</u> and how the situation was resolved:

B1: BOK group – see case A12

The dominant female was missing on May 3, 2006. There was no breeding activity for 295 days, until February 22, 2007, when a new female was able to join the group after the dominant daughter ZATA disappeared; once she joined, she chased away the younger daughter STLV.

B2: EST group

The dominant female was missing on January 3, 1999. There was no breeding activity until May 5, 2000, when the daughter of the group was chased away by a coalition of three females from outside the research area ("barbarians").

B3: HAK group

The dominant female was missing on January 2, 1996. There was no breeding activity till February 22, 1997, when two daughters of the group disappeared, then a female from elsewhere joined, and the two remaining daughters were chased away by the newcomer.

B4: HNK group

The dominant female was missing on July 9, 1999. There was no breeding activity till April 20, 2000, when the four daughters of the group disappeared and a new female joined the group.

B5: KEN group

The dominant male was missing on May 2, 1987, and there was no breeding activity until February 1, 1988, when LVTM joined the group. LVTM was a son of the group that left it in December 1982. When he returned, the dominant female was not his mother. One male and one of the females had left the group before LVTM returned, and two moved to another group shortly after he returned. One son remained with his mother who was the dominant female, and left the group the following Fall. These developments can be explained by suggesting that all group members recognized LVTM as a former group member, even though none of them was in the group when he had left in 1982. The daughters did not consider him a potential mate, and the remaining son did not fear being chased away. The dominant female had come from another group. The most reasonable explanation is that LVTM was visiting the group from time to time and was accepted when visiting, and that the younger babblers came to know him as one of the group. There was a similar situation in the POL group, where a daughter of the group that had left four years earlier returned to it: here, too, the reasonable explanation is that the group members recognized her as belonging to the group (see 10b about LTVS and her father in the POL group).

There are scores of cases in the database where babblers returned to their groups after years of being away; they should be identified and examined to see the manner in which they returned.

B6: MTE group situation 1

The dominant male of the MTE group was missing since August 15, 2005, and there was no breeding activity through June 11, 2006. The first male that tried to enter the group failed. The second male – AGTZ, see 4a – was supported by the mother of the group and her daughters. He entered the group slowly and carefully, and ended up fighting each of the two sons individually. The sons joined the nearby ZVA group and shortly after chased away its dominant male GTVL (see a detailed description of the sequence of events in the article "ALTS – the life of a female babbler" by Amotz and Avishag Zahavi in the Hebrew publication חיות וחברה vol. 35 pp. 56-62).

B7: MTE group situation 2

When the breeding female ALTS disappeared in November 2011, the group contained 5 females and 5 males of various ages. Many females, particularly from neighboring groups, tried to join the group but were chased away by the daughters. AGTZ, the father of the group, as well as his oldest son, copulated with some of these females but did not leave the group. The following Spring each of the daughters joined another group where she could reproduce, and this enabled a new female to join in February 2013 with her two daughters. The father, AGTZ, lost a year of reproduction, but gained in having his existing offspring mature safely, and indeed most of them ended up producing his grandchildren.

B8: MZR group situation 1

The breeding female disappeared on August 6, 1987. On December 2, 1987 the dominant male disappeared as well. The group that remained contained 4 males and 3 females, all of them offspring of the male that disappeared which had been the dominant male in the group for 10 years. On April 15, 1988 a female from outside the research area joined the group, and one of the daughters disappeared. The new female started building a nest, but it was destroyed right away, and she disappeared a week later. Again the group that remained was all siblings and could not breed. Only the following Spring, in March 1989, two new females managed to join the group, and the two daughters who remained till that time disappeared.

B9: MZR group situation 2

The two daughters were chased away by two females who joined from outside the group.

B10: POL group – father-daughter pairing

LTVS hatched in the POL group in Spring 1981. Her parents – the female MHTA, originally from the BOK group, and the male SMTA, originally from TMR group – were the dominant pair of the POL group for 8 years, from Spring 1981 to December 1989. LTVS stayed at POL, her natal group, until she was five years old, and then moved to the SVA group, after which she was the breeding female in the BBS group. This group fell apart in winter 1980 and LTVS went back to the POL group in Spring 1990, after her mother disappeared. When LTVS came back, the group included 2 males and 4 females, all of the descendants of the dominant male and siblings of LTVS. Father and daughter bred together and had two daughters together.

This series of events includes three unusual events: a: a father breeding with his daughter – though after four years in which they were in different groups; b: LTVS was able to join the group even though it already had four adult females – normally adult group members fight and prevent an outsider of the same gender from joining the group; and c: all four adult daughters remained in the group after LTVS rejoined it – normally adult group members of the same gender disappear during the fighting against a newcomer, or are chased away soon after. Eventually, later in the year, two of the females moved to another group and two disappeared, but that's normal – as a rule, females leave their natal group and seek a group where they can breed.

Events b and c can be easily explained if we assume that LTVS was recognized by group members as one of the group, rather than as a stranger trying to take it over — even though most group members had not yet hatched when LTVS left the group. We have seen above a case of a male who returned to his former group as the dominant male (see LVTM in KEN group, case b5 above). He, too, re-entered the group without opposition or expulsion.

This explanation of events b and c, that is, that the group recognized LTVM as one of the group, does not explain event a – that is, forming a breeding pair with her father. Since this is a very unusual case, there is another possibility – that her father was not the father of her offspring. There is no recorded observation of LTVS actually copulating with her father. Perhaps this is similar to a case we have seen in the MTE group -- as we describe in detail in the article about

ALTS (in Hebrew). In that case in the MTE group, the eldest son, HTVL, expelled his father, helped his mother build a nest, and accompanied her. Since we were aware of the rarity of such a situation, we made sure to observe them closely, and indeed saw the mother ALTS meeting the expelled former dominant CTAS, who was not with the group but remained nearby. It may be that LTVS' offspring also had a different father than her own father who was the dominant male in the group.

There are recorded cases of babblers from different groups copulating while away from their respective groups. It will take searching to find out whether the females laid any eggs, and if so, where. We believe that this is another question that can be researched through recorded observations.

B11: TLB group

A new female joined after the mother of the group left.

B12: TMR group

Seven months after the breeding male disappeared, the mother of the group and her daughter left the group; a month later a new female joined the group.

Discussion

The benefits of adoption

Babblers from outside the group cannot easily join an existing group. When adult babblers join a group, it almost always involves fighting, overcoming, and expelling all existing adult group members of the same gender. Fledglings, on the other hand, are welcomed even when they are youngsters who require feeding and care. Sometimes the group initiates such joining. It is easy to claim that this "benefits the group" by increasing its numbers without the investment required in the first, difficult month of raising young. But in our opinion, "benefit to the group" can't explain why an individual babbler would invest for the "benefit to the group" when it is not in its own individual interest.

We believe that fledglings are accepted because they pose no threat to group members: they join at the bottom of the social ranking, that is, below every individual currently in the group. In each group, there is a rigid social ranking for each gender. In this ranking, each individual's position is determined by age: the older outranks the younger. Fledglings of the same nest fight over the ranking between them during their first few weeks of life; the ranking set at that time typically remains as long as they are members of the same group. The position of each individual in this social ranking determines the course of its life. Each benefits from having others below him or her in this social ranking, as long as they do not compete over food or another resource. In addition to that, feeding others and taking care of them provide social prestige to the care giver (see detailed discussion in the 1990 article and in the book).

Avoidance of mating with offspring of one's group

Out of thousands of male-female breeding pairs that have been documented over the years of research, there is one documented case of a father breeding with his daughter, after the daughter was outside the group for five years (case B10, POL in the table). There was one other case that was observed by Amotz Zahavi but not documented in detail, where a mother copulated with her youngest son, when her older sons prevented males from the outside from joining the group and thus prevented her from breeding. It is possible that a few other cases may be found by thorough searching in the database. We don't know of any case of a brother and sister breeding together in their group of origin; we have two cases where a brother and a sister bred together when they met each other again in a different group. In both cases the brother and sister knew each other in their group of origin, but left it separately. Again, we assume that a thorough seach of past observations may bring to light a few more cases. We have shown and discussed avoidance of mating within the group in table 5, with twelve cases of groups that did not breed for long periods when all adults were offsprings or siblings of all other group members.

On the other hand, we have found that eight out of the twenty-five cases of adoptees that reached over a year in age, bred with their adoptive parent, or at least copulated with their adoptive parent, even though they joined the group at a very young age. In fact, such a mating took place every time that conditions allowed it.

We believe that these observations show that group members know and remember that the adopted individuals joined the group from the outside, and that breeding with them is allowed. This means that there is individual, long-term relationship between babblers, and their behavior shows a difference between acceptable and unacceptable breeding mates.

Further questions:

Adopting within a group

The data about adopted babblers was collected during a thorough review and correction of data for each babbler in our database. In all, we have found 42 cases of adoption, and only half of them survived over a year. Even though the numbers are small, it appears that the difference between breeding with them within the group, in contrast with the avoidance of breeding with offsprings of the same group, is clear and well-defined.

One can enlarge the pool of examples by examining also cases where adults join a group that includes young fledglings. Adoptions by one group of a nestling or a fledgling of another group are not common. It is quite common, however, to find an adult or a group of adults taking over a group, chasing away the breeding individual and all other adult members of the same gender, and taking their place. Such cases usually happen during breeding season, and often when the group has nestlings or young fledglings. In many cases, these newcomers help raise the group's young, even though these are not their own offsprings (we posit that taking care of the fledglings provide prestige to the care-givers). The relationship of a newcomer to the group's

offspring is similar to that of an adopting parent to a fledgling that joins a group from another group. Since such cases are far more common than cases of adoption, it may make sense to identify them and see whether the adult who joins eventually breeds with individuals that it raised from a very young age. An example we have found is case A21, of TVPA and his adopting mother GTZA in the HNC group.

Other questions:

Many other questions came up while researching this material. Were there other cases of mating between parent and offspring when one of them returned to the group after a long time away – as in POL (case B10)? Were there such matings when the parent and offspring found themselves together in another group?

Another matter worth investigating is the breeding of siblings with each other. We have been on the lookout throughout the research for siblings breeding together in their natal group, and have not found any. But we have documented two cases of such breedings when the two were in another group, several years after one or both of them have left their natal group. In both cases we checked and found that their time in their natal group overlapped – that is, they have known each other in their natal group. The examples we have found are LGPT(=ALPT) and HCAT, originally from the MTE group mating in the BOT group, and CTAA and PTVZ originally from the POL group, mating in the KAN group. There may be other such cases that we have not identified yet.

We have also found two cases in which individuals returned as breeders to their natal group after years away from it: LVTM in the KEN group (case B5) and LTVS in the POL group (case B10). In both cases, when they rejoined their natal group they did not chase away the adults of the same gender who were in the group, unlike the norm when an adult babbler joins a group. Cases of individuals returning to their natal group are not rare, and should be identified and checked carefully.

These questions indicate complex, long-term relationships between individuals. It is not rare to observe an individual who left of its own volition (that is, was not expelled) revisiting its natal group, or returning to it, with no conflict involved. There were also cases of individuals moving back and forth between two groups before settling in one of them (see GHGT, case A12). Even individuals who were chased away or expelled may meet with former fellow group members from time to time; usually, such meetings end when the individual who did the chasing or expelling joins the scene. In other words, an individual who was chased away is still considered a group member by members of the group who were not involved in the chasing away. This means that such individuals can get to know newly-hatched members of their natal group, who were not in the group before the individual left it. In the article about ALTS two such cases are described: CTAS, the previous dominant male who was chased out by HTVL, would meet with his former group-mates and even copulate with the breeding female, yet get away whenever HTVL came near; and years later the younger daughter TPAL, who was chased out by her sister

GTVC, kept trying to rejoin the group and was accepted by other group members but not by GTVC, who each time chased her away again.

Such cases are important for understanding social connections between individuals, social relations, memory, and behavior based on assessed future possibilities among babblers.

These kinds of questions cannot be answered by short, one-year field studies for a master's thesis or even 2-5 year long field studies for a PhD. One can utilize many years of past observations, as in this current study; quite likely many events were not recorded in detail when they happened because they were not recognized as important at the time. For this reason, it is important for all who study the babblers to be aware of such questions and to take care to record their observations with as much detail as possible when they happen.

At the present time (October 2021), the study of the Arabian babblers at Hatzevah is headed by Dr. Oded Keinan at The Arabian babblers research, Dead Sea and Arava Science Center -- see https://www.zahavibabblers.com/. Yael Alon continues to observe and record the current babbler population in the study area.

You can reach Dr. Avishag Kadman-Zahavi at <u>Avishag.Kadman.Zahavi@gmail.com</u> and Naama Zahavi-Ely at <u>Naama.Zahavi.Ely@gmail.com</u>

	Nor	n-adopted babl	blers mention	ed in this study:			
From: Bsic dat	a plus new.XLS	S	מהקובץ:				
ID	Name	שם	SEX	natal Gr	Group	Ringing Date	SYNONYM
4685	ALAT	אלאט	F	SAL	SAL	21/3/03	
			F		SAL		
3214	ALTS	אלטש		SAL		13/5/94	
5175	APTV	אפטו	М	???	ELU	17/8/10	
5693	ATLH	אטלח	F	???	KVS	13/10/14	
5234	ATPA	אטפא	М	???	HIL	30/11/09	
4880	CTAA	כטאא	М	POL	POL	7/5/06	
3119	CTAS	כטאש	М	MTE	MTE	13/3/94	
5533	CZCT	כצכט	М	HIL	HIL	8/4/14	
4103	GLTL	גלטל	М	BOT	ВОТ	20/3/97	SLTL
4590	GTVL	גטול	М	MIZ	ZVA	15/6/01	
4683	GTZA	גטצא	F	SAL	HNC	21/3/03	
3120	HCAT	חכאט	М	MTE	AHM	13/3/94	LHAT
5186	HHTS	חחטש	М	???	ELU	19/9/10	
4626	HTAZ	חטאצ	F	???	BOK	6/1/02	
5602	LATG	לאטג	F	KVS	KVS	15/7/14	
4102	LGPT	לגפט	F	MTE	MTE	4/3/97	ALPT
1113	LTVS	לטוש	F	POL	POL	15/4/81	
4564	LVTL	לוטל	F	MEA	HNC	6/3/01	
1138	LVTM	לוטם	М	KEN	KEN	14/3/81	

5182	LVTP	לוטפ	М	ARU	KVS	22/8/10	
5424	LZVT	לצוט	М	HOR	HOR	2/5/13	
4917	PTVZ	פטוצ	F	POL	KAN	4/7/06	
1492	SMTA	שמטא	М	TMR	POL	16/4/79	
5755	SPAT	שפאט	F	???	BER	1/7/15	
5191	SSZT	ששצט	F	???	HIL	19/11/10	
4739	STLV	שטלו	F	BOK	BOK	13/3/04	
4366	THHG	טחחג	М	BOK	BOK	14/3/98	
5193	TPLL	טפלל	F	???	ELU	19/11/10	
4565	TSAL	טשאל	F	MEA	BOK	6/3/01	
5455	TVAP	טואפ	F	POL	HIL	27/6/13	
4810	TVPA	טופא	М	HNC	HNC	15/3/05	
5265	TVSZ	טושצ	F	HIL	BER	12/6/11	
5439	VSAT	ושאט	М	ARU	KVS	9/6/13	VSTA
4681	ZATA	צאטא	F	BOK	BOK	20/3/03	